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THE UNIVERSITY OF ALBERTA

A MODEL TO DETERMINE POSSIBLE ADAPTIVE STRATEGIES FOR THE ABORIGINAL EASTERN TREELINE DENE

by

© Patricia Alice McCormack

A THESIS

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "A Model to Determine Possible Adaptive Strategies for the Aboriginal Eastern Treeline Dene" submitted by Patricia Alice McCormack in partial fulfilment of the requirements for the degree of Master of Arts.

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ABSTRACT

The thesis discusses various problems involved in hypothesizing pre-fur trade adaptive strategies for the aboriginal Dene who lived in the treeline area from the headwaters of the Coppermine River to the mouth of the Churchill River. General archeological and ethno-historical parameters for this aboriginal population are delimited.

The analysis emphasizes an ecological approach, and careful attention is paid to physiographic and climatic factors, since it is their interaction that essentially determines the plant and animal populations. The effects of glaciation on the Canada Shield are outlined in terms of their consequences for soil, soil drainage, habitats, and migration routes. The discussion of climate is focused on the pronounced seasonality of the area and the impact of the seasonal cycle on species distribution, with particular attention paid to the various effects of snow.

Physiography and climate determine the nature of the plant and animal communities. There are three plant subzones described, each relating to climatic factors: the Shrubby Tundra Subzone of the colder tundra, the Lichen-Woodland Subzone of the warmer boreal forest, and the Forest-Tundra Subzone, the ecotone between the two. Each is defined and described with regard to the habitats and plant communities it contains. The relationships of the plant communities to

substrate is made explicit. The role of fire in the forest is related to post-fire plant succession and its effects on animal distribution.

Animal populations are divided into primary consumers or herbivores and secondary consumers or predators. The distribution of species for summer and winter, on tundra and in forest is summarized. Emphasis is placed on the annual seasonal cycle of barren-ground caribou and moose and their different habitat preferences, relating these to the habitat preferences of the other forest herbivores. Predator distributions are related primarily to those of their prey. Fish are discussed separately because of their distinctive aquatic habitat.

Hypothesizing the human adaptation to these resources rests theoretically on the concept of technoenvironmental advantage or efficiency and the concept of redundancy. Suitable "prey" species for a hunting and fishing oriented population are selected, and the number of possible options available to humans based on these prey are calculated. The options are gradually reduced in number to a small list that differs from summer to winter, and from the forest to the tundra. From this set of options the range of winter and summer adaptive strategies is hypothesized, as well as probable demographic correlates.

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about a human population from ecological data. He provided useful criticism about the model as it related to Athapaskans in particular.

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CHAPTER 1

INTRODUCTION

In 1670 the Hudson Bay Company ship Wivenhoe sailed to the mouth of the Nelson River on a trading expedition (Rich, 1942:210). This brief voyage led to others that culminated in the establishment of two important fur factories, Port Nelson or York Factory and Churchill or Fort Prince-of-Wales farther north at the mouth of the Churchill River. The latter post was established specifically to trade with the "Northern Indians," the Dene or Athapaskans ranging over a huge triangle of land extending from Churchill to Lake Athabasca and north to the headwaters of the Coppermine River. They would become known later as Yellowknives and Chipewyans.

Although the Northern Indians were mentioned in Company reports from at least 1680 (Rich, 1948:14), the first good cultural description did not occur until Samuel Hearne's three trips into the interior in 1769 to 1772, a century after the earliest possible contact date, 1670. Therefore his narrative does not describe the aboriginal lifestyle, but that of people who were apparently increasingly involved in and adapted to the fur trade. It is extremely difficult, if not impossible, to sort out what was aboriginal from what was a reaction to the fur trade in the data Hearne

provided.

The Problem

June Helm (1965:362) stated that "the nature of the socio-territorial arrangements of these Athapaskans in aboriginal times we can never truly know." However, she felt she could equate nineteenth century social structure with that of the pre-contact, aboriginal period because there was no "evidence that a significant alteration in organizational structure has occurred between earlier and contact-traditional horizons" (Helm, 1965:362).

James Smith made the same assumption when he detailed four cultural phases for the Brochet Chipewyans. He said that "culture change during this period [the early fur trade period] was probably minimal," although he had just allowed that "little detail is known" about the earlier aboriginal period (J. G. E. Smith, 1970:60). In brief, he assumed that these Chipewyans had always depended almost entirely on barren-ground caribou as their subsistence base. He did not examine the problems inherent in a caribou-oriented economy, especially those problems of continual access, nor did he explore other possible subsistence strategies.

Smith and Helm's statements are untenable; it is incorrect to assume either the presence or absence of change if the preceding state of affairs is largely unknown. Further, in an earlier article, Helm had said that in even the earliest descriptions "it is evident that the contact

situation had already wrought changes in the aboriginal way of life" (MacNeish, 1956:132). Her different statements are contradictory. They are interpreting the aboriginal period in terms of the ethnographic present despite the evidence that there had usually been significant changes in adaptive strategies by native groups as responses to contact with Europeans:

> . . . it is now recognized that aboriginal peoples, especially in the New World, were influenced by European commercialism earlier than was previously assumed. Much of what was formerly considered to be aboriginal represents an early phase of acculturation, a relatively viable synthesis of old and new that preceded the severe shaking up or outright destruction of Indian societies (Leacock in Damas, 1969:1).

For the Dene, the main agents of culture change were the Europeans and their trading posts, which became "prodigious new resources placed upon the land" (Helm et al., 1971:22). The Dene became one of many groups for whom the aboriginal lifestyle is largely unknown.

In the absence of fieldwork with living informants, there are approaches which might be used to solve the problem of how to reconstruct the period before the fur trade, the aboriginal situation: the ethnohistorical, the archeological, and the ecological. Unfortunately for the first, historical records are often biased, distorted, incomplete, or simply too late, as with Hearne. Furthermore, it is difficult to validate what are inherently subjective accounts. Archeological approaches are also inadequate simply because there has been too little research done in

Dene territory.

Parameters

However, archeological and ethnohistorical materials can provide some general parameters for the aboriginal situation. The Northern Indians were the people of the Taltheilei Shale Tradition (ca. 200 B.C. to the historic period), characterized by the use of grey silicious shale for tools and weapons. This tradition is found around the east arm of Great Slave Lake, far out on the tundra at Aberdeen Lake, and in northern Saskatchewan (Noble, 1971:110-115; Wright, 1972:82-83). In northern Manitoba there is a similar tradition, with quartzite rather than shale prevalent. Though appearing later in time (after 500 A.D.), it too is considered to be Dene (Nash, 1970:81-85).

These ancestral Dene populations made a variety of lithic tools: scrapers, bifaces, points, lanceolates, knives, hammerstones, and circular chi-thos, among others, using in the western regions a small amount of native copper Bone was used also to make harpoons, punches, and possibly fleshers (Noble, 1971:110-115; Nash, 1970:81-85).

A 1716 report from Knight at York Factory provides some early historical substantiation for the archeological evidence (Hudson Bay Company [H.B.C.], B.239/a/2:28):

> . . . there is an abundance of Indians in those parts as never has hade either trade or commerce with any people but as use bone, beaver teeth flintstones for weapons of warr with there bows and arrows.

Those Indians would at that time have included the Northern Indians. Knight reported also the use of a great deal of copper, though on second hand information. In summary, the ancestors of the historic population, the Northern Indians, were characterized by a lithic-bone technology.

They were characterized also by a hunting-fishing orientation. Limited prehistoric faunal evidence indicates that these people were eating caribou, black bear, beaver, dog or wolf, swans, and fish (Noble, 1971:114; Nash, 1970: 83). All the early ethnohistorical data emphasizes the primary dependence of the Northern Indians on caribou and fish, following the caribou on a year-round basis on their migrations between the tundra and forest. Their territory possessed few moose and few fur-bearers, with beaver very scarce (Hearne [orig. 1795], 1958:51,135; Dobbs, 1744:46; Jérémie [orig. 1732], 1912:9).

The first impact of the fur trade appeared early: the Southern Indians or Maskegos (Swampy Cree) went to war with the Northern Indians, driving the latter north (Doughty and Martin, 1929:28; Tyrrell, 1931:265; H.B.C., B239/a/2:22). Following the establishment of the Churchill post, the Northern Indians began to participate in the fur trade. While in 1719 they did not know how to dress furs properly for the fur trade and had few furs to trade, by 1720 a large number of Dene came to the post to trade (H.B.C., B.42/a/1: 48,80). This number grew each year.

By the time of Samuel Hearne's trip to the Coppermine River in 1770-1772, nearly everyone had been affected by the fur trade, although they were still hunting caribou. He observed, in fact, that there had been a great deal of culture change. Nevertheless, it can be seen that the Northern Indians were characterized in the early historical period and certainly in the aboriginal period by a hunting and fishing lifestyle, with gathering of plant foods relatively unimportant.

Ecological Reconstruction

These general technological and economic parameters can be used as bases for ecological reconstruction, the third approach to hypothesizing the aboriginal situation. The broader framework for such an approach is human or "cultural ecology." Human ecology emphasizes adaptive and exploitative relations, through the agency of technology, of the human group to its habitat, and the demographic and sociocultural consequences of these relations (Helm, 1962: 63). More specifically, I want to deduce from the technological and economic parameters and an examination of the environment what Julian Steward called the "'logical potentialities'" of an area. These are

> ". . . a function of the local ecology, that is, the interaction of environment, exploitative devices, and socio-economic habits. In each case, the exigencies of making a living in a given environment with a specific set of devices and methods for obtaining, transporting, and preparing food and other essential goods set limits

> to the dispersal or grouping of the people and to the composition of settlements, and it strongly influenced many of their modes of behavior" (Steward in Harris, 1968:659).

In other words, the most important variables in this sort of study are the environment, technology, and economy. It is the interaction among these three factors that sets limits on other social possiblities.

Steward proposed three procedures for analyzing societies from this perspective. Because I am working with an extinct culture rather than with an observable one, however, I must substitute "deduce" where Steward writes "analyze":

1. [Deduce] the interrelationship of exploitative or productive technology and environment.
2. [Deduce] the behavior patterns involved in the exploitation of a particular area by means of a particular technology.
3. Ascertain the extent to which the behavior patterns entailed in exploiting the environment affect other aspects of culture (Steward [orig. 1955], 1972:40-41).

Steward tried to reconstruct Chipewyan social organization on the basis of this model. He hypothesized that treeline Dene would live in large composite hunting bands because of their primary reliance on large herds of migratory game animals, barren-ground caribou and musk-ox, in an area that would support relatively few people (Steward [orig. 1955], 1972:143-144,147). His reconstruction was incorrect because of the contradictions in his argument: while his basic premise was that treeline Dene relied primarily on these large herds, he nevertheless went on to

explain that in fact such large herds were hunted "more or less seasonally" (Steward [orig. 1955], 1972:147) by large population aggregates of temporary duration. This situation resulted from the fact that large herds of caribou occur at treeline only at certain times of the year, not on a year-round basis. Either his knowledge of the environment was incomplete and/or faulty, or he ignored some of the evidence. Further, he did not examine the nature of the smaller groupings that must have resulted when the Dene were not hunting the large herds, perhaps because he had denied a priori that kinship could be a basis for group formation for people living in composite bands (Steward [orig. 1955], 1972:143).

Another example of an ecological approach using this framework was Harvey Feit's reconstruction of Mistassini Cree aboriginal lifestyle (1969). His description of the boreal environment was accurate and broad, but he based his analysis of human exploitation on the restrictive supposition that a human population would remain in a region throughout most of an entire successional cycle, a single zone strategy. His use of what seems to be a faulty premise invalidates his reconstruction.

Nevertheless, both Steward and Feit used what seems to be a useful approach, one that I wish to use to hypothesize about possible adaptive strategies for the eastern treeline Dene. Using a modified ecological approach

to reconstruct aboriginal lifestyle assumes first that the habitats* can be reconstructed. Since the habitants of ca. 1670 in Dene territory were most probably the same as those of today, reconstruction will be relatively simple. The basis for this assumption will be discussed later. Secondly, and as a corollary, in this case it is assumed that the aboriginal population was not altering its environment significantly; that is, the influence of the Dene on their habitat was so minimal that their removal from parts of it would produce no important changes in the relationships among habitat components. These human inhabitants were hunters and gatherers, operating at a lithic-bone level of technology.

Present Analysis

There are three steps in the procedure; first, various ecosystems** must be carefully described in terms of components potentially significant for the human population, which means, basically, tracing the significant food chains. Obviously, the more complete the description, the less the chance that an essential ingredient will be omitted. Equally obvious, not all components can be included. The ecosystems described will be defined in terms of more-or-less "dominant"

---

*Habitats are the places where plants and animals are usually found, such as aquatic habitats (Odum, 1971:234).

**An ecosystem is a unit that includes the organisms and physical environment of a given area, interacting in definable fashion. The extent of this unit is defined arbitrarily (Odum, 1971:8).

species.

Secondly, the possible ways a human population could fit into the ecosystems of the area will be posited, based on the nature of the resource base. The evaluation of the possibilities will include Marvin Harris' concept of techno-environmental efficiency or advantage (1971:203-217) and Alexander Alland's concept of redundancy (1967:126). The number of adaptations is finite, with some more feasible than others. The most practicable adaptations have specific implications for annual economic and settlement patterns and for some aspects of demography. It is not likely that socio-cultural systems can by hypothesized, as there are no absolute correlations between types of social structure and economic base. Essentially these two steps correspond with Steward's first two, and they overlap with his third.

My third step, beyond the scope of this paper, would be to validate the model by examining the independent archeological data and by building models of culture change that could be validated ethnographically.

Therefore the thesis of this paper is that certain aspects of aboriginal Chypewyan-Yellowknife lifestyle, and by extension, any aboriginal inhabitant in the area, can be hypothesized or "reconstructed" by building a model of probable pattern of resource use based on the possible adaptations to the various ecosystems and by hypothesizing the effects of this pattern of use on human movement and

demography. While such an endeavor has implications for the more general problem of predicting aboriginal lifestyle, this paper is specifically an attempt to hypothesize on logical grounds what a particular aboriginal lifestyle might comprise.

CHAPTER 2

KEEWATIN HABITATS AND ECOSYSTEMS

A description of habitat and ecosystem involves two main aspects: the physical conditions and the plant and animal inhabitants. All animals depend ultimately on plants for food, at different trophic levels. Although they in turn affect vegetation, the major limiting factors for vegetation are physical: physiography and climatic regime, two variables independent to a certain degree. It is the interaction of these two that determines which plant and animal species will inhabit the Dene area.

The study area is that region traditionally occupied by Chipewyan and Yellowknife Indians, bounded roughly by the Churchill River, Lakes Reindeer, Wollaston, Athabasca, Great Slave, Dubawnt, and Nueltin, and the headwaters of the Coppermine River (Fig. 1). The physical features of the land are relatively permanent and homogeneous and do not directly determine the climate, which has fluctuated greatly over time.* I shall begin with the former as the least unchanging and therefore the most predictable.

A. PHYSIOGRAPHY

Between Hudson Bay and the Rocky Mountains there are

*Physiography will modify or alter various aspects of climate, but it does not determine the most important one for the Keewatin area: the temperature regime.

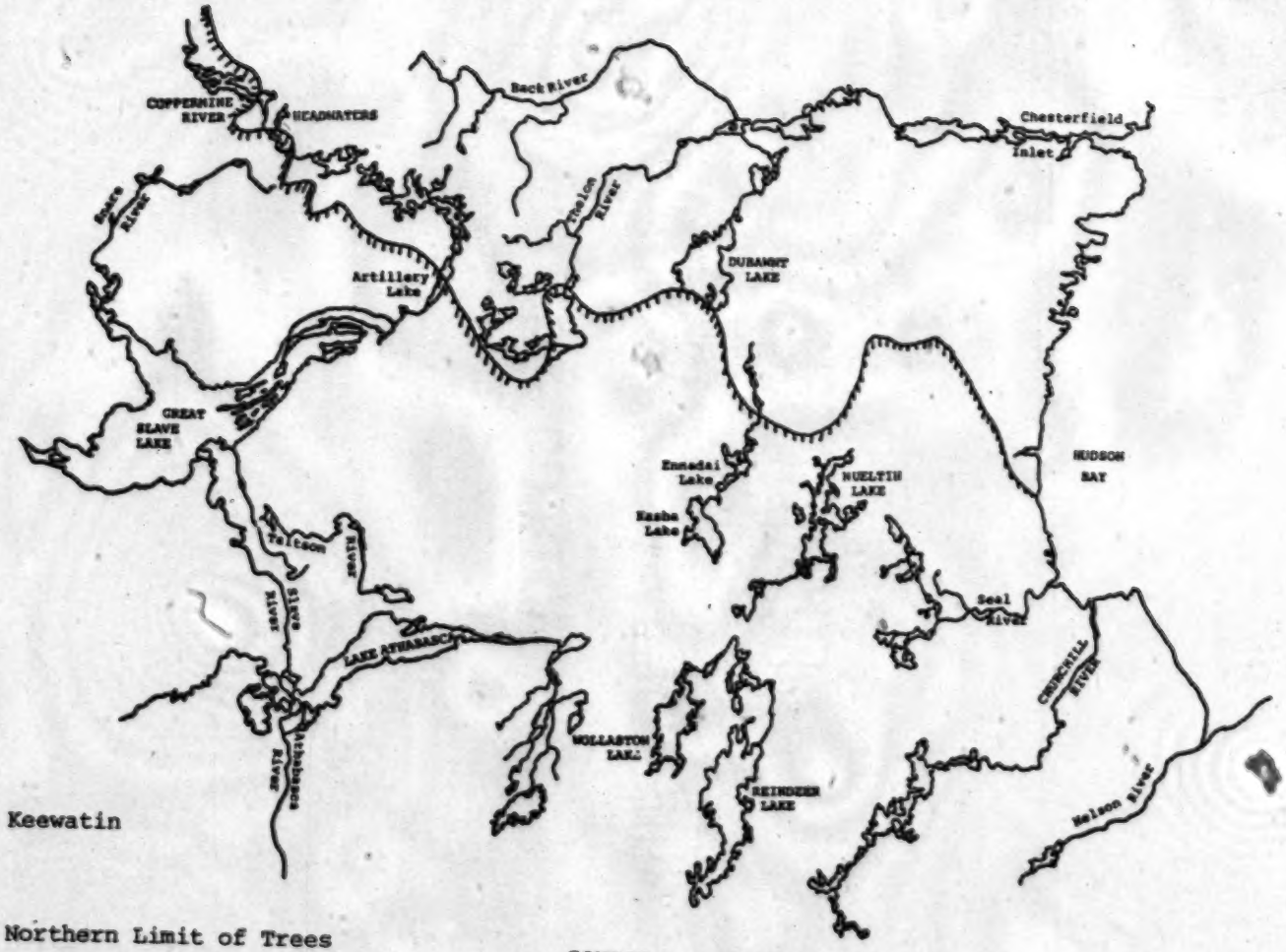

Figure 1

Map of the Keewatin Region

||||||| = Northern Limit of Trees

SOURCE: KELSALL, 1968

two major physiographic divisions, the Canadian Shield and the Great Central Plain. The relatively distinct boundary between them is defined by the contact of Paleozoic sedimentary rocks to the west (the Great Central Plain) and by pre-Cambrian crystalline or metamorphic rocks to the east (the Shield). This boundary runs from Lake Winnipeg up through Lake Athabasca, the valley of the Slave River, and through Great Slave Lake, roughly coinciding with and always including the western edge of the study area. It is the Shield which provides the physical setting (Harper, 1931:18; MacKay, 1955:13). The entire Canadian Shield is actually much larger than this small portion, which can be specified further as the Keewatin Section of the Laurentian Upland Province or Plateau. The Laurentian Plateau extends east and south of Hudson Bay as well as to the west (MacKay, 1955: 14). Both the "Canadian Shield" and the "Keewatin Section" will be used to refer to the study area.*

That part of the Shield that is the Keewatin is, like all the Shields, composed largely of pre-Cambrian rocks, the result of early volcanic activity and mountain building, that now form a stable core area within the continent. The rocks are divided into a stratigraphic succession, dominated by granites and gneisses (Good, 1955:316; Lees, 1959:3):

---

*This Keewatin Section is not to be confused with the political district of "Keewatin, N.W.T."

a. Archaean--granite, lavas, minor amounts of sedimentary rock and their metamorphic equivalents
b. Early Proterozoic--quartzite, slate, phyllite, dolomite
c. Late Proterozoic--dacitic lavas, pyroclastic rocks, conglomerates, and arkose.

There have been four major sources of surface change in the Shield: the first has been deposition. The Shield edges and sometimes portions of the interior may be covered by younger sedimentary rocks laid down by shallow seas in low-lying areas. For example, the region directly south of Lake Athabasca lies within the Shield, yet it is covered with sandstone (Harper, 1931a:19).

The second source of change has been erosion, the converse of deposition. The Shield has been subjected to erosional forces throughout the long period since its formation, wearing the surface down into a peneplain, a broad, low surface (Good, 1955:316). Both deposition and erosion go on over time.

Thirdly, at the close of the Tertiary this peneplain was uplifted and warped around Hudson Bay to give it a saucer-life shape, with a central depression in the Hudson Bay area. The Keewatin Section thus slopes downward from west to east, affecting overall drainage patterns (MacKay, 1955:16).

The final and probably most important source of change in terms of effects on the vegetation was Pleistocene glaciation, with the last glacier receding less than 10,000 years ago. Camsell described its effects in describing the

Tazin Highlands, an area on the western edge of the study area (Camsell, 1916:13):

> One of the most marked features of the region is the evidence of the intensity of the glaciation with the resulting freshness and unweathered characteristics of the rock surface. The rocks are everywhere rounded, grooved, striated and, even in the beds of streams where erosion and obliteration of glacial markings would be expected to be most rapid, striae still remain. In general, the region is characterized by glacial erosion and removal of material rather than by glacial deposition. Deposits such as boulder clay, moraines, drumlins, sand-plains, while present, are not as widespread as in the region further south and west, and, consequently, streams have little sediment to carry [emphasis added].

Thus the first effect of glaciation was to scour the surface, removing all soil. In many places the area has a thin drift cover of till with numerous outcrops of bedrock, while in others glacial landforms such as drumlins, eskers, and small moraines cover the bedrock surface (Lee, 1959:4-6), representing more widespread glacial deposition than in the Tazin Highlands area. Sedimentary deposits such as alluvium form slowly unless streams originate outside the Shield, such as the Athabasca-Slave River system. Because of the hardness of the bedrock and most of the rocks of deposition, mineral soils will also form slowly.

Glaciation's second effect was to disturb drainage patterns and create innumerable lakes (MacKay, 1955:15). Most rivers today have no well-defined valleys or evenly graded profiles. For example, the Taltson River is characterized by a series of level stretches and short, abrupt falls (Camsell, 1916:11). Because of the hardness of the rock and

the short time since glaciation, a well-developed drainage system has not yet been able to form, despite the large rivers that do flow through the area (McFadden, 1965:9). The many lakes are usually shallow basins with smooth, rocky shores and bottoms. In other words, they are low spots in the bedrock that have filled in with water (Camsell, 1916:18).

In summary, the Keewatin Section presents a picture

> . . . when viewed broadly . . . of a broad plain . . . . In detail, however, it is very irregular, broken, and rocky . . . . It is a country also of numerous, rock-bound lakes, which occupy all the lower levels, and of streams flowing in ill-defined and irregular valleys. The intervening areas are rocky . . . hills, which rarely rise more than 200 feet above the lakes or rivers and are, as a rule, less than 100 feet high (Camsell, 1916:15-16).*

Some implications for plant and animal distribution and growth can be derived. First, because there is generally a poor substrate with little or no soil and few good chances for sedimentary deposition, plants will be inhibited or limited according to their ability to tolerate such a meager nutrient base and shallow substrate. Secondly, conditions of disturbed drainage and the prevalence of many lakes will be important in determining both suitable habitats and possible migratory water routes into the area in the post-Pleistocene period for aquatic animals and for those using ice on which to travel, such as caribou.**

---

*This description is of the Tazin Highlands in particular, but it is characteristic of the entire area.

**Present drainage patterns differ greatly from early post-glacial drainage patterns.

Finally, disturbed drainage may mean that precipitation will not be quickly lost through run-off, at least not in low-lying areas.

B. CLIMATE

The climate since glaciation has been generally stable in the Keewatin Section. There have been some cooler and warmer periods as evidenced by shifts north and south, respectively, of vegetation zones, but with no obvious changes in types of vegetation. For at least the last 300 years, even the location of these zones seems to have remained about the same as they are today, indicating that the climate has not fluctuated markedly in that period (Nichols, 1967; Nichols, 1968; Bryson, Irving, and Larsen, 1965; Larsen 1965).* If the physiography defines the substrate, it is the climatic regime that further limits species distribution by factors such as annual cycles of temperature and precipitation.

The annual climatic pattern results ultimately from the annual increases and decreases in the amount of solar energy available to heat the land surface. In the fall, the number of daylight hours decreases, making an increasingly smaller amount of solar energy available. This trend is reversed in the spring (Ragotzkie and McFadden, 1962:19).

---

*The relationship between climate and vegetation zones will be discussed later.

The two major seasons that result, summer and winter, are each preceded by transitional seasons, spring and fall. Spring begins with "thaw," and fall, with "freeze-up."* These two indicators of the annual temperature cycle that defines the seasons will be discussed later.

The Seasons and Temperature Regime

The seasons differ in length and in definition between forest and tundra in the Keewatin Section. Spring is defined as beginning when the daily mean temperature rises to 0°C (Kendrew and Currie, 1955:76). It ends with the beginning of summer, and so it can be defined further as that period when temperatures range from 0°C to 10°C (50°F) in the forest and from 0°C to 4.4°C (40°F) on the tundra. In the forest, spring begins with the advent of these warmer temperatures in approximately April and lasts through May, while on the tundra or treeless zone it lasts for only one month, June (Kendrew and Currie, 1955:76-77,101-102).

Summer is defined differently in each area: in the forest it is the period when the mean monthly temperature is greater than 10°C (50°F) in each month, generally the three months of June through August. Tundra summers are so much

*"Break-up" rather than "thaw" may seem to be the more logical opposite to "freeze-up." However, freeze-up and thaw both respond directly to air temperature, whereas break-up is a consequence of thaw and therefore characterized by a time lag. The establishment of permanent snow cover that occurs with or follows freeze-up may also be characterized by a time lag. It is therefore not a good indicator of temperature regime.

cooler that the criteria are mean monthly temperatures over 4.4°C (40°F) but less than 10°C (50°F), for July and August only. Such warm periods determine the length of the growing season for plants (Kendrew and Currie, 1955:77,101-102).

The end of summer is signalled by the drop in temperatures that introduces fall for two months in the forest, September and October, and for one month on the tundra, September. Fall is the reverse of spring, in that it is that period when temperatures range from 10°C (50°F) to 0°C. in the forest, and from 4.4°C (40°F) to 0°C on the tundra. Fall is actually never defined in the literature (Kendrew and Currie, 1955); the definition used here is one that is consistent with the other definitions of seasons and with temperatures at freeze-up.

Winter occurs when the mean monthly temperature is less than 0°C in each month, lasting from November through March, five months, in the forest, while on the tundra it lasts for the eight months of October to May (Kendrew and Currie, 1955:76,101). Obviously all seasons may begin earlier and/or end later, and "unseasonal" temperatures may occur in all.

Freeze-up and Thaw

In the north, freeze-up refers usually to rivers and lakes. Its opposite is break-up. Because these phenomena are easily studied and dated, the literature on this aspect of climate (temperature regime) tends to concentrate on the

aquatic environment. The seasonal indicators for the terrestial environment are the establishment of permanent snow cover that accompanies or follows freeze-up and its loss by "thawing" in the spring. Since both indicators are more difficult to study and date, neither is used as much in analyzing seasonal sequences. The following discussion will reflect the consequent differences in the literature.

Freeze-up (referring to ice) and thaw (referring to snow) are equivalent phenomena, in that both are thermal events in response to the beginning of fall and spring. They reflect the prevailing temperature conditions. Ice will form on all small lakes as soon as the daily mean temperature drops to 0°C, corresponding with the temperature changes accompanying fall. Conversely, snow begins to waste rapidly when the daily mean temperature rises to 0°C, defined as the start of spring (Currie, n.d.:14).

Were the ice surface not covered with snow, it too would begin to waste. Since the snow must melt first, however, there is a time lag between the beginning of spring thaw and break-up. Conversely, though temperatures in the fall may be freezing or less, there will be no permanent snow cover established until there is precipitation.

During both freeze-up and thaw there is a line north of which all lakes are frozen, and a second line south of which all lakes are open. Between these two lines is a transition zone in which some lakes are open, some frozen, and some partly open and frozen. It is known as the lake

freezing zone during freeze-up (McFadden, 1965:15; Ragotzkie and McFadden, 1962:1-2), and conversely, as the lake thawing zone during the thaw (dates for this zone would lag behind dates for the onset of "thaw").

Freeze-up

The lake freezing zone's two boundaries are established by differences in freezing times of shallow and deep lakes. Freezing can occur only after the entire water column has cooled to "well below" 4°C (Ragotzkie and McFadden, 1962: 9). Water cools by losing heat to the atmosphere through radiation, evaporation, and turbulence or eddy diffusivity (Currie, n.d.:3). Such cooling may be delayed by the mixing of top water with warmer subsurface water where the stirring action of currents is significant (Currie, n.d.:4). Also, large, deep lakes have a greater heat content and will thus respond more slowly to climatic changes than will smaller lakes (Ragotzkie and McFadden, 1962:10; Peterson, 1965:25).

The southern boundary or shallow lake freeze-line represents the more rapid cooling and freezing of lakes with a mean depth of about one to three meters. These lakes may freeze and thaw many times before final freeze-up (McFadden, 1965:16,62; Ragotzkie and McFadden, 1962:10). The deep lake freeze-line, the northern boundary, includes most of the deeper and thus slower to cool and freeze lakes, ranging from 6.5 to 10 and even 15 meters in maximum depth. There is good agreement between the freezing dates of these deep lakes and

the date the forty day mean air remperature falls to 0°C. Therefore the shallow lake freeze-line corresponds roughly with the onset of fall, with its drop in temperatures, and the deep lake freeze-line with the beginning of winter and increasingly colder weather. The latter line corresponds also with the southward movement of continental Polar air, which will be discussed later. The deep lake freeze-line advances south much more slowly than the shallow lake freeze-line (McFadden, 1965:16; Rogotzkie and McFadden, 1962:9).

There are a few lakes which are anomalous in that their response time to climatic change is much greater than that of any of the other lakes due to their size. In the Keewatin Section these include Great Slave, Dubawnt, Nueltin, Reindeer, Wollaston, and Athabasca Lakes (McFadden, 1965:16). This annual pattern of freezing remains relatively the same from year to year, although the times and locations may differ slightly, corresponding with annual differences in season (McFadden, 1965:33).

When freezing begins, ice tends to form from the outside to the middle. Once a layer is formed, it increases in thickness throughout the winter due to the conduction of heat from the lower to the upper surface, where it is lost to the atmosphere. Total thickness may be as great as 2.4 meters (8 feet) (Currie, n.d.:3,12-13).

Thaw

Although "thaw" refers primarily to snow and

terrestial conditions, its most visible effect is break-up of the ice. After the relatively opaque snow cover has disappeared due to the spring rise in temperatures, the winter ice cover creates a greenhouse effect by trapping the increasing amounts of radiant energy. Because the amount of energy trapped in lakes varies only with the surface area, shallow lakes will warm and thaw faster than deep ones (Ragotzkie and McFadden, 1962:10; McFadden, 1965:76). Secondary factors include wind activity, currents, runoff of melting snow from the surrounding land, and absorption of heat by the dark or muddy banks, creating open leads along the shores. Deep lakes tend to open first around estuaries of rivers running into them and wherever currents have limited the thickness of the ice (Currie, n.d.:4,8-9).

The differential thawing time for deep and shallow lakes creates a lake thawing zone. Its northern boundary is the shallow lake thaw-line, north of which all lakes are still frozen, and its southern boundary is the deep lake thaw-line, south of which all lakes are open (McFadden, 1965: 15-16). The large, anomalous lakes would thaw later than the remainder of the larger lakes.

Because the thaw process involves radiative heating from within rather than transfer of heat to the atmosphere, the main cause of cooling, there is poor agreement between mean air temperatures and break-up (McFadden, 1965:109-110). However, wastage of snow does begin when the daily mean

temperature rises to 0°C, and there is generally good agreement between dates of break-up and the "running" mean air temperature of 4.5° to 5°C (40.1° to 41°F) for deep lakes (McFadden, 1965:76), approximately the temperature for the beginning of the tundra summer. So perhaps the northern movement of the lake thawing zone could be considered to correspond with the northern movement of spring and summer, at least for the tundra.

The general trend of both freeze and thaw lines is northwest to southeast, which agrees with the direction of vegetation zones (McFadden, 1965:46). The close relationship between climate and vegetation in the Keewatin will be drawn more explicitly later in the paper.

Precipitation

Precipitation falls as rain or snow, depending on the temperature. Total yearly precipitation ranges from 12 to 16 inches, usually decreasing as one goes north. There are simply too few sources of moisture available to support heavy precipitation levels.

Winter is characterized by persistent high pressure or anti-cyclone conditions over the Keewatin (Currie, 1953:2) which weaken in the spring when more moisture is evaporated, making the atmosphere less stable. There is then an increase in cyclonic activity which leads to more frequent storms throughout the spring, summer, and fall (Currie, 1953:3; Kendrew and Currie, 1955:85). July and August have the most

rain, followed by fall, especially in areas where large bodies of open water add to the instability of the air as they cool with the decreasing fall temperatures. There is a third level in April and May (Currie, 1953:16; Kendrew and Currie, 1955:85). Although 30-50% of all precipitation occurs as snow,* ** most snowfall occurs in spring and fall, not in winter, with January and February generally the driest months of the year (Currie, 1953:17, Fig. 1).

In this area, the small amount of precipitation per se is not a limiting factor for plant growth, which will be explained in the discussion about permafrost. The fact that the annual snowcover is both deep and long-lasting is highly significant, however, with two major consequences, the first for plant and animal winter habitat and the second for albedo and air mass formation.

Snow Cover and Habitat

The nature of the snow cover affects habitats differently in the forest and on the tundra. The forest snow cover is basically a thick, fluffy emulsion of snow and air that is relatively uncompacted since the trees prevent the wind from shaping it. When new-fallen, its specific gravity may be under 0.05. Such snow provides a good

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*10 inches snow = 1 inch rain.

**The proportion of precipitation that falls as snow increases the farther north one goes. It may well be over 50% in much of the Keewatin Section.

insulating blanket for the soil, which will remain relatively warm, moist, and stable (Pruitt, 1970:85-86).

Tundra snow, on the other hand, is characterized by its having been disturbed and moved by the wind. Snow particles are consolidated into a hard mass, then worked and reworked by the wind. The results are moving snow and a succession of drift forms (Pruitt, 1970:93). Such conditions affect the depth, density, and even the presence of snow.

Both types of snow cover provide certain types of winter environments for plants and animals. Many plant species, such as white spruce (Picea glauca), grow best where snow is very deep. They need insulation from the cold, drying air found in both tundra and forest as well as protection from the wind-driven snow crystals on the tundra. Small mammals such as shrews, mice, and occasionally squirrels must live in the warm subnivean environment because they are physiologically incapable of producing enough body heat to offset the loss to the cold air above. Therefore it is the snow cover which permits the survival of the small but most important herbivores of the food chain (Pruitt, 1970:86,88). It follows, then, that there should be more suitable habitat for such animals and thus more animals (absolute numbers and numbers of species) in the forest than on the tundra with its more variable snow cover. Consequently, the total range of small mammals and their predators should be significantly smaller on the tundra.

The type of snow surface should also affect animal distribution, since animals in the forest have to cope with deep, soft snow, whereas tundra animals have heavily-crusted

snow or even no snow on which to travel. There should be special behavioral, phsyiological, or morphological adaptations in many animal species to such long, cold, and snowy conditions. On might expect to see animals migrating to the forest from the tundra for the winter season in search of game or more suitable snow environments.

Snow Cover and Albedo

The second effect of snow cover is to affect the amount of albedo, or reflectivity of the earth surface. More specifically, surface albedo is "the ratio of reflected to incident solar radiation at the earth's surface" (McFadden, 1965:77). Since what is not reflected is absorbed and converted to sensible heat, the amount of albedo is important in determining surface temperatures.

A snow-covered surface has a high albedo value, about 90% on the tundra, because nearly all solar radiation is reflected. The albedo is about half that in the forest due primarily to the masking effect of conifers (Ragotzkie and McFadden, 1962:17-18). All tree foliage, and especially that of conifers, shields snow-covered ground and readily absorbs incoming radiation. Albedo will increase to the extent that conifers are draped with snow, or qali. In large measure, the albedo differences depend on the presence or absence of above-the-snow vegetation, especially trees, and on the openness of the crown because of its effects on the visibility of the snow cover (Hare and Ritchie, 1972:346; Ragotzkie and McFadden, 1962:16).

Lakes can affect the albedo strikingly, from a very low value of 5% or less for an unfrozen water surface to a

very high value for a snow-covered ice surface (Ragotzkie and McFadden, 1962:16), especially in a region where water can cover up to 20% or more of the land surface (McFadden, 1965: 9). Because they do not differ significantly in distribution between forest and tundra, however, they will have the same effects in each. Still, the presence of a large number of lakes and gali in a forested area may serve to introduce a tundra-like albedo into that area. For much of the winter the forest may be as cold as the tundra, though without the wind.

Forest vegetation has an important effect on climate in that the lower forest albedo permits faster warming in the spring than for the tundra. In turn, there is a direct feedback effect on vegetation since a longer season with above-freezing temperatures means a longer growing season (Hare and Ritchie, 1972:353-354).

Air Mass Formation

The temperature regime and changing amounts of albedo are the main factors affecting air mass formation. An air mass is a "naturally occurring atmospheric complex" characterized by "a certain temperature range in each place and season, and characteristic moisture, turbidity and structure as well" (Bryson, 1966:229). Fronts or frontal zones are the relatively distinct boundaries between two air masses (Bryson, 1966:229).

The characteristics of an air mass are determined by

the constant movement and change of radiation (insolation), heat (latent), and water vapor between the air and the earth. The rate of air mass formation and the causes of change in it are functions of the nature of the ground surface and the time the air remains over that surface (Ragotzkie and McFadden, 1962:19). Thus each air mass will have a characteristic location, bounded by the mean location of the fronts between it and adjacent air masses. The land surface covered by it will be distinguished by its relatively homogeneous air mass regimen (Bryson, 1966:229). In the Keewatin Section there are three major air masses; the continental Polar air mass is present during the winter, and it is replaced by two air masses in the summer: maritime Arctic and Pacific.

The continental Polar air mass forms over the tundra in autumn. When the albedo rises drastically with the first snow, there is a sharp decline in surface heating. Both the land surface and the air above it will cool rapidly by radiation. Because the tundra becomes a high pressure area, drier and more stable as the lakes freeze, the air can remain over the tundra long enough to take on its identifying characteristics of very cold, dry, and stable (Ragotzkie and McFadden, 1962:19; Hare, 1955:64).

This air mass can move easily across the tundra, unmodified by any surface heating. As it moves over the forest, the increased forest heat due to lower albedo and still open water areas slows down its southward movement by

eroding the leading edge, adding heat and moisture. The degree of winter cold is thus ameliorated by and for the forest, and the onset of winter is delayed, as evidenced by the slow southward movement of the deep lake freeze-line. Eventually even the forest freezes up completely, however, and winter is characterized by a continental Polar air mass regimen over the entire Keewatin.

When the snow melts and the land warms in the spring, the winter air is replaced with two air masses, one, maritime Arctic, originating over the Arctic ocean and the other, Pacific air, having its origin over the Pacific. Maritime Arctic air is cool and unstable, while the second air mass brings warm Pacific air from west of the Cordillera (Bryson, 1966: 232; Hare, 1955:64-65). The summer location of each has important implications for soil temperatures and permafrost and for vegetation, with its feedback effects on climate.

Permafrost

Permafrost is "perenially frozen ground" (Péwé, 1967: 27). It can be defined as any earth materials, wet or dry, that are colder than 0°C from at least one winter to the next (Brown, 1970:129). Permafrost develops when more heat leaves the ground than enters, and it is therefore generally confined to areas in which the mean annual temperature of the air near the ground surface is below 0°C (Jenness, 1949: 157).

Not surprisingly, the southern limit of the zone of continuous permafrost corresponds approximately to the mean July location of the Pacific-Arctic front; it defines a region continually overlain by cool to very cold air. South of the front lies a zone of discontinuous permafrost in which frozen ground is found where vegetation can insulate it from solar radiation (Brown, 1970:129). Also, trees that shade the ground and intercept some of the snowfall that would normally insulate the ground from the winter cold may lead to the formation of a permafrost lens beneath the trees. Moss and peat cover are good insulators when covering already frozen ground (Brown, 1970:133-134; Jenness, 1949:14-15).

Permafrost consists of two parts: a layer of ground, often very thick, which is frozen summer and winter, and overlying it, a second active layer, one that thaws each summer. The depth of this active layer depends on the mean annual temperature, the heat conductivity of the soil, and the insulation afforded by plants (Jenness, 1949:14; Brown, 1970:129).

It is largely the presence of permafrost that modifies the effect of the small amount of annual precipitation in the north. The exposed or shallowly covered bedrock of the Shield adversely affected subsurface drainage; permafrost furthers this effect by providing an impervious layer a short distance below much of the land surface. Therefore drainage is confined to the shallow active layer, leading to

water-logged terrain in low areas (Jenness, 1949:23; Brown, 1970:134-135; Currie, n.d.:19). In an area that by rights should be arid or semi-arid, the disturbed drainage makes available an adequate supply of moisture to the rootzone. In fact, only hydrotrophic species will grow in lower areas (Péwé, 1967:48; Jenness, 1949:24).

Permafrost affects also soil stability and the temperature of soil within the rootzone. Probably the second most important effect for vegetation, however, is the shallowness itself of the rootzone, limiting plant growth to those species with shallow or very flexible roots as well as a tolerance to poorly drained soils. Within the forest, black spruce (Picea mariana) and tamarack (Larix laricina) are the two trees that do best in such a substrate; they are well adapted to poorly drained, shallow substrates. On the other hand, birch (Betula papyrifera) have shallow root systems but need well-drained soils, as do white spruce (Picea glauca), pine (Pinus banksiana*), balsam poplar (Populus balsamifera), quaking aspen (Populus tremuloides), and alder (Alnus crispa) (Currie, n.d.:19; Jenness, 1949: 23-24; Péwé, 1967:48).

Climate and Vegetation

It is through permafrost conditions that climate affects plant growth indirectly. Climate has a more direct

*Recently renamed Pinus divaricata (Hare and Ritchie, 1972:335).

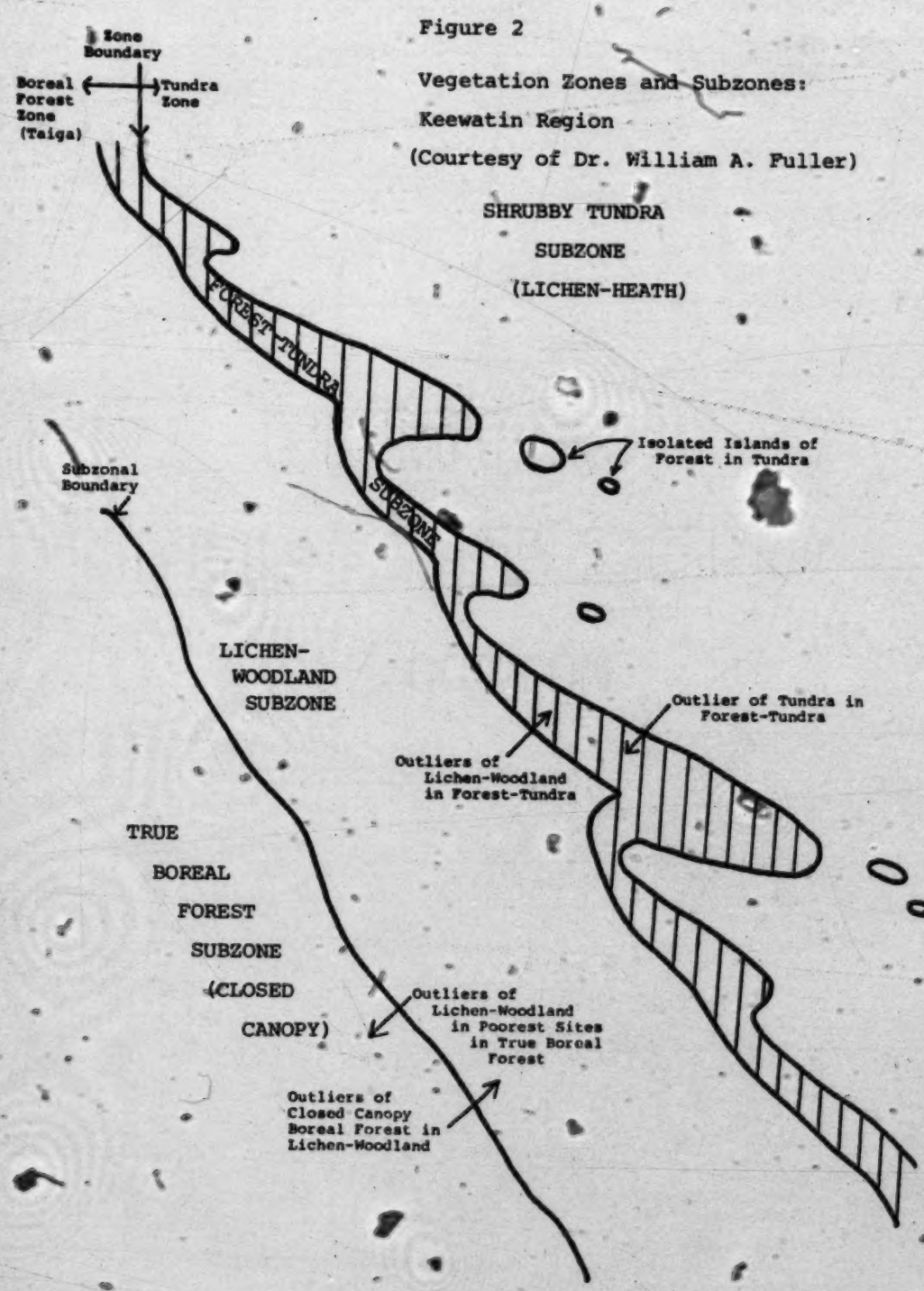
effect on above-ground vegetation through snow conditions and the length and warmth of the growing season. It is to be expected, then, that there will be zones of vegetation corresponding to at least summer air mass regimes and therefore also to permafrost zones, all comprising a matrix of interrelated components. In fact, the Pacific-Arctic summer front, as represented by the 10°C isotherm, does coincide closely with the forest-tundra boundary, the treeline (Bryson, 1966:234). The rather abrupt transition from trees to no trees is the most striking effect of climate on vegetation, although there are changes in other plant species as well. Underlying the area dominated by the summer Arctic air mass regimen is the tundra zone, and to the south is a forest zone underlying the summer Pacific air (Larsen, 1967: 1). It is summer climate that is significant; the winter climate is effectively homogeneous throughout the area despite varying degrees of cold.

C. VEGETATION

The treeline meanders from the northwest to the southeast, paralleling the lake freezing-thaw zone and coinciding with the Arctic front. It forms the southern boundary of the Tundra zone of vegetation and the northern boundary of the Boreal Forest or Taiga. Each zone is divided into subzones, of which three comprise the study area (see Fig. 2). The relevant part of the Tundra Zone is the Shrubby Tundra

Figure 2

Vegetation Zones and Subzones:
Keewatin Region
(Courtesy of Dr. William A. Fuller)


Zone Boundary
Boreal Forest Zone (Taiga)
Tundra Zone
SHRUBBY TUNDRA SUBZONE (LICHEN-HEATH)
FOREST-TUNDRA SUBZONE
Isolated Islands of Forest in Tundra
Subzonal Boundary
LICHEN-WOODLAND SUBZONE
Outlier of Tundra in Forest-Tundra
Outliers of Lichen-Woodland in Forest-Tundra
TRUE BOREAL FOREST SUBZONE (CLOSED CANOPY)
Outliers of Lichen-Woodland in Poorest Sites in True Boreal Forest
Outliers of Closed Canopy Boreal Forest in Lichen-Woodland

Subzone, the southern tundra bounded by the treeline. Technically, the other two subzones, the Lichen-Woodland and the Forest-Tundra, are part of the Boreal Forest (LaRoi, 1967: 229). The northern boundary of the Lichen-Woodland Subzone corresponds with the treeline, while the Forest-Tundra is actually an ecotone between the two adjacent areas. These three vegetation subzones will be defined briefly, then each will be described in terms of the habitats and plant communities it contains. This description will include an explanation of the role of fire in the Lichen-Woodland Subzone.

Three Vegetation Subzones

The Shrubby Tundra Subzone is typified by low shrubs, sedges, lichens, and herb species. There are a few outliers of trees north of the treeline, which mostly represent relics from earlier warmer periods when forests grew further north. These clumps were in favorable locations and managed to escape the fires that destroyed the trees around them; they would not now regenerate if destroyed (Bryson, Irving, and Larsen, 1965:47; Larsen, 1965:57; Sorenson et al., 1971:468-469).

The forested region south of the treeline is the Lichen-Woodland Subzone.* It is characterized by widely

*Other names: Taiga, Hudsonian Zone, Open Coniferous or Lichen Forest, Boreal-Lichen Forest (Dansereau, 1955:86; Ritchie, 1962:25-26; Britton, 1967:72; La Roi, 1967:229)

spaced spuce and an understory dominated by mats of lichen among the trees and a discontinuous layer of shrubs under the trees (Larsen, 1971a:151; Baldwin, 1953:115-116). The True Boreal Forest Subzone farther south is dominated by a closed crown forest, with lichen-woodlands restricted to dry, unproductive sites (La Roi 1967:229). This subzone is outside the study area and will not be discussed in detail.

Finally, there is an intermediate Forest-Tundra Subzone that reflects local physiography, soils, and variation in location of the front, among other factors. Frontal conditions will prevail with greatest frequency along the mean position, but they occur also to the north and south, though with decreasing frequency, creating a climatic transition zone (Larsen, 1967:2). The southwestern boundary of this zone is the forest border, probably corresponding roughly to the usual southern penetration of the Arctic air mass. The northeastern boundary is the actual limit of trees, which is determined both by the northernmost penetration of Pacific air in summer and by topography, since rugged areas with many outcrops like the country east of Great Slave Lake provide protected areas for trees (Larsen, 1971a:152). Also, trees grow in long fingers along all river valleys.

Within this subzone lichen-woodland occurs in discontinuous stands on sheltered slopes, river banks, and esker slopes. Exposed sites such as summits of till ridges and

hills are characterized by tundra (Ritchie, 1959:36; Baldwin, 1953:123). In other words, this subzone is one in which forest communities can grow if sheltered. To the northeast the environmental climatic complex exceeds the tolerance limit of the trees as well as of many shrub and herbaceous species (Larsen, 1971a:178). The exact reasons for this vegetation-climate relationship are still not understood.

These three subzones have been characterized by climax vegetation found on mature and well-drained upland surfaces (Tedrow and Harries, 1960:241). Actually, each subzone consists of several plant communities, which are "aggregations of native plants which behave essentially independently of one another" (Larsen, 1966a:3).* They can be measured either qualitatively, by species composition, or quantitatively, by frequency or abundance of each species. Unfortunately, there are no good maps of species distribution of geographic inventories except for specific areas within the larger region (Ritchie, 1962:5). Furthermore, there are variations of the "expected" pattern caused by historical factors, local topography, and fire disturbance. In lowland areas, drainage seems to be perhaps more important than climate in determining community types (Ritchie, 1962:25). A general picture of the climax or mature plant communities can be drawn, however, and the effects of the major

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*Community means more generally all the plant and animal populations that inhabit a given area (Odum, 1971:5).

disturbance, fire, on these patterns can be described.

With climatic regime held constant in each zone, the other factors to be considered are edaphic ones, that is, conditions relating to the nature of the substrate, including drainage conditions. The physical substrate includes in both areas four general types: the first is rock or sand, including bedrock, till, eskers, and other glacial deposits. Secondly, there are mineral soils, podzols in the forest and Arctic Brown Soil on the tundra. Podzolic soils are acidic, relatively infertile soils typical of northern coniferous forests. They are characterized by a leaching of iron and organic materials from upper to lower soil horizons. In the Keewatin these soils are restricted largely to areas that are or were once forested, including large stretches north of the present treeline (Larsen, 1966a:1-2). Arctic Brown is a strictly Arctic soil found on well-drained uplands that shows little leaching of the surface layers (Tedrow and Hill, 1955; Tedrow and Harries, 1960). Thirdly, alluvial deposits can be found along stream and river edges and at river deltas. Finally, organic terrain underlies many wet communities.

The short, warm season and long, cold season mean that the rate of decomposition of organic materials will be very slow, as will be the release of nutrients. Arctic and Subarctic soils in general have a low natural productivity, and they are especially poor in nitrogen. Plant growth will

be inhibited accordingly (Tikhomirov, 1959:5).

Drainage conditions can be divided into three general categories: (1) very dry, supporting xerophytic vegetation, (2) well-drained with mesophytic vegetation, and (3) wet conditions where drainage is poor due to blockage, a shallow active permafrost layer, or other factors, in which hygrophytic vegetation thrives (Dansereau, 1955:87).

Shrubby Tundra Subzone

In its simplest configuration, shrubby tundra vegetation can be defined as consisting of three communities: rock fields, tussock muskeg, and low meadows. There are also three main communities limited to eskers: summits, slopes, and kettles.

The best drained community is the rock field, found on till or mineral soil on upper slopes and summits. In these areas there is up to 20% of exposed bedrock and boulders, between which there is finer till and shallow accumulation of surface organic material. The smallest gravel material has been removed by wind and water erosion. This community is always well-drained and even dry. It is dominated by heath shrubs, dwarf willows and birches, lichens, mosses, and herbs (Tedrow and Harries, 1960:241; Larsen, 1965:41; Larsen, 1971a: 159).

Patches of tussock muskeg can develop in small depressions in rock fields, but the tussock muskeg communities are located generally on lower or intermediate slopes which

may appear almost flat, but must have enough drainage to eliminate the possibility of standing water such as one finds in the meadows. They are also always associated with a very shallow active layer. The community is characterized by hummocks underlying tussocks of sedges and grasses, with lichens often growing on hummock summits. Tussock muskeg becomes rarer as one goes north from the treeline, replaced by a more abrupt transition from low meadow to rock field (Larsen, 1965:43-44,54; Larsen, 1971a:160-163).

The most poorly drained is the low meadow community, typically found in low, flat areas where water can accumulate, especially spring meltwater, often lasting into summer. Permafrost is both greater in depth and closer to the surface due to the absence of insulating peat and the greater amount of heat transport from the meltwater. Lichens are rare here, and the plant list is relatively short. Sedges are a dominant form, associated with willow, some heath shrubs, and mosses. Willow (Salix spp.) and dwarf birch (Betula glandulosa) may be found where the meadow grades upward into tussock muskeg (Larsen, 1965:44; Larsen, 1971a:163-165).

Esker communities resemble very closely those on till or mineral soils. The driest are those of the summit, where wind and desiccation lead to an "extreme paucity of individual plants" (Larsen, 1971a:165). Summit communities are characterized by species adapted to pioneering on sandy areas under inimical conditions, especially a high degree of wind

erosion and unstable surfaces. These include lichens, herbs, and a few sedges (Larsen, 1965:46).

The nature of slope communities depends upon their direction and whether the slope is steep or gentle. South or southeast-facing slopes receive more sunlight and are also more protected from cold, since they are leeward to the winter prevailing winds and thus are covered by deep snow accumulations. Conversely, north or northwest-facing slopes receive less sunlight and are more exposed, leading to differences in the frequency of growth of plant species, though not in the type of species. Vegetation includes dwarf birch, shrubs, lichens, grasses, and some mosses (Larsen, 1965:46-47). Gentler slopes are intermediate between rock fields and esker slopes in their vegetation, which include higher frequencies of some shrubs.

Finally, kettles are depressions often associated with impeded or blocked drainage that may be filled with ponds and hydrotropic vegetation, especially horsetails (Equisetum spp.), herbs, sedges, and willows (Larsen, 1965: 47).

Lichen-Woodland Subzone

Vegetation in the Lichen-Woodland Subzone is distinguished first by the presence of trees. There are seven important species which I shall describe briefly before discussing the various plant communities, both climax and subclimax.

Black spruce (Picea mariana) is the dominant and most widespread species within the Lichen-Woodland Subzone. It occurs over a wide range of substrate types, from very dry rocky hills to muskegs, and is relatively undemanding for nutrients. However, it does prefer sites protected from prevailing winds where snow accumulates to a considerable depth in winter (Larsen, 1971a:151,153; Baldwin, 1953:115; Harper, 1931b:99; Ritchie, 1959:40). Black spruce is easily destroyed by fire because of its thin bark and flammable foliage, yet it is nevertheless adapted to fire in that its semi-serotinous cones are opened by fire. Cones will survive most fires to germinate well on the newly exposed mineral soil, and black spruce can also reproduce by layering. Black spruce is usually established by fire, indicated in part by the high volume and rapid growth in fire-origin stands (Kayll, 1968:4; Scotter, 1964:65).

Often associated with black spruce and dominant in young communities is tamarack (Larix laricina), and their ranges are coextensive. It is a hardy conifer that is also found in a wide range of substrate conditions, both in muskegs and other swampy areas and to a lesser extent on drier ground (Harper, 1931b:98; Ritchie, 1959:37-40; Baldwin, 1953:115), both in undisturbed and in fire-origin stands (Kayll, 1968:6).

White spruce (Picea glauca) is fussier and less widely distributed, since it needs better drainage and

nutrients than does black spruce or tamarack. It grows well on glacial till of granitic origin and on sand deposits along shorelines, preferring alluvial or dolomitic materials. It will not grow in muskeg. Where protected and where snow can accumulate in winter, it can grow quite large. White spruce is relatively common in the western edge of the region, in the Lake Athabasca-Great Slave Lake area, perhaps because there is more outcrop and alluvial soil, thus providing more of the nutrients it needs. Conversely, it is rare in the Nueltin-Reindeer Lakes area except on eskers; the till to the east is not rich enough in minerals (Larsen, 1971a:150-152; Baldwin, 1953:115; Harper, 1931b:98). White spruce is not very fire resistant, tree or cone, but it will germinate well on exposed mineral soil if not exposed to strong light, with the seeds probably coming from adjacent, unburned stands (Kayll, 1968:4). Its limitations make white spruce a less hardy and more poorly-adapted conifer for this zone than the first two.

The final conifer to be found in the area is the jackpine (Pinus banksiana), which typically grows in drier, well-drained areas (Baldwin, 1953:115). It is a classic fire-adapted species, as it requires fire to open its serotinous cones and to burn off the cover from the mineral seedbed where it establishes its seed. Jackpine can be found growing in nearly pure stands on sandy soil following fire, though it later becomes relatively rare. The northern

limits of its range are well south of the treeline in the east, at least 100 miles south of Ennadai Lake (Kayll, 1968: 5; Harper, 1931b:98; Scotter, 1964:64; Ritchie, 1959:40). Today, pine is the characteristic conifer in much of the Lichen-Woodland around the east arm of Great Slave Lake. Whether this situation is due to increased burning in recent years or reflects special edaphic conditions that would have been aboriginal as well is undetermined. Although black spruce is considered to be the most characteristic conifer in the Lichen-Woodland, it should make little difference for the surrounding plants and the animal inhabitants if it is replaced by white spruce or jackpine.

The three main deciduous trees do well in specific locales, but they would not be considered climax species. White birch (Betula papyrifera) will grow on rocky hills and low, sandy shores, if well-drained. It prefers well-watered sites with good drainage and can become dominant locally. These trees are common, though not plentiful, in the entire region (Baldwin, 1953:115; Harper, 1931b:101). They are a common pioneer species following fire because of their light, easily disseminated seed. Their leaves, like those of all the deciduous species, contribute to the renewal of ground litter following fire, leading to improved conditions for lichen growth (Kayll, 1968:5; Scotter, 1964:65).

Quaking aspen or aspen poplar (Populus tremuloides) avoids low, damp ground to grow on hills or on dry valley

soil. Its frequency differs locally: it is abundant in the Lake Athabasca-Great Slave Lake area but scarce in the Nueltin-Reindeer Lakes region, perhaps corresponding, like white spruce, to a need for good nutrients. Its northern limit is about the same as for the jackpine, south of the treeline (Baldwin, 1953:115; Harper, 1931b:100; Ritchie, 1959:40). Aspen poplar is also a good pioneer species following fire since its seed is easily spread by wind and perhaps more importantly, a light to moderate burn will stimulate aspen suckering (Kayll, 1968:6).

Finally, balsam poplar (Populus balsamifera) is found on banks and lake shores, preferring recently-deposited alluvial soil. It is scarce and widely scattered in the Nueltin-Reindeer Lakes area but common on the proper soils in the Lake Athabasca-Great Slave Lake region, perhaps reflecting the greater amount of alluvium found in the latter (Baldwin, 1953:115; Kayll, 1968:6; Harper, 1931b:100). The tree is protected from fire by its thick bark, and it has a light, wind-disseminated seed (Kayll, 1968:6).

In areas not disturbed by fire, black spruce is considered the dominant species, though white spruce or jackpine may be more prevalent in certain areas. Major types of topographic climax communities include black spruce-lichen forests, fens, bogs (muskegs), eskers, and lake-river margins.

Black spruce-lichen forests, the definitive communities for the Lichen-Woodland Subzone, occupy mineral soils under xeric and mesic conditions.* The structure and

*"Xeric" refers to very dry conditions; "mesic," to conditions of medium moisture.

composition will vary according to whether it occurs on slopes or on summits, but both are dominated by black spruce (and white spruce and jackpine in the west) associated with varying numbers of jackpine, birch, and tamarack. In northern Manitoba the black spruce are in open stands with a density of about seven trees per 100 square meters. This density will depend upon the suitability of conditions for spruce growth. Beneath the crown are a discontinuous shrub layer and a ground cover dominated by lichens in a thick carpet. There are smaller amounts of herbs and mosses, especially at the base of the trees. Mosses are very rare on summits, with their greater exposure and usually shallower substratum, but they increase greatly on lower, well-drained mesic sites. The proportion of shrubs increases also, making the vegetation less parklike with a correspondingly sparser lichen cover (Baldwin, 1953:115-116; Argus, 1966:122-123; Ritchie, 1959:9-13).

Areas with impeded drainage are characterized by organic terrain with bog or fen conditions. Bogs or muskegs* are communities poor in nourishment that are sustained primarily by rain or melted snow that cannot drain off. Vegetation is ombrotrophic and poor in number of species, defined primarily by heath shrubs restin on a more-or-less continuous stratum of sphagnum moss (Sphagnum spp.) which

*"Muskeg" is distinguished from "tussock muskeg" by its lower pH, its moss substrate as opposed to the cotton grass (Eriophorum) tussocks of tussock muskeg, and by the presence of trees, mainly black spruce and tamarack.

has formed a mat of vegetation over the undrained water. Lichens can often be found on raised hillocks, and black spruce and tamarack will grow in these wet, poorly nourished regions. When trees are present they may be termed "bog forests" (Ritchie, 1959:14). Muskegs are common around small inland lakes and in extensive zones between fens and black spruce forest in level stretches (Ruuhijärvi, 1970:319; Sjörs, 1963:55,61,64; Moss, 1953:448; Dansereau and Segadas, 1952: 490-491,493-494; Argus, 1966:123-124; Baldwin, 1953:118).

Fens, on the other hand, exist in areas of impeded drainage that are better nourished: they have intermittent to constant contact with water that has been in contact with mineral soil, deriving often from drainage from muskegs. Even "poor" fens, which are usually adjacent to ombrotrophic parts and may be dominated by the same species, will have an increased number of plants needing this richer substrate, while the rich fens are characterized by markedly minerotrophic species, including sedges and willows. The foliage is light green, contrasting to the brown muskeg dominated by sphagnum mosses. Tamarack may be scattered on drier parts, such as ridges. Bogs may exist within fens at topographically suitable sites. Fen conditions are too wet to allow lichen growth except in bog palsas. There are many transitions between bog and fen which occur along gradients of soil moisture conditions and sources. Ponds and shallow lakes may be surrounded by swamps and marshes, and they are found in the

sheltered bays of bigger lakes and in slow-moving stretches of rivers (Ruuhijärvi, 1970:319; Sjörs, 1963:55,62; Moss, 1953:448; Baldwin, 1953:119; Ritchie, 1959).

Esker vegetation comprises the same three communities as for the tundra: summits, slopes, and kettles. Summit communities are often unstable, with few or no trees, and subject to erosion, possibly caused partly by lack of protective snow cover in the winter due to winds (Ritchie, 1959:20-25). In those instances, vegetation will be characterized by pioneering species on sandy soils, especially grasses and herbs (Larsen, 1965:46; Ritchie, 1959:21). Where stable or on slopes, the vegetation is that of an open white spruce or black spruce-lichen forest, with relatively rich ground vegetation, especially in lichens, and associated shrubs. Birch is often present (Argus, 1966:126; Ritchie, 1959:21-22,25). Kettles may contain pools and different types of vegetation depending on the nature of the drainage. White spruce is always absent from these usually poorly drained sites, but black spruce may be present (Ritchie, 1959: 22; Argus, 1966:126).

The main difference between esker vegetation and lichen-woodland on mineral soil is the presence of white spruce as characteristic of the former. However, black spruce does replace white spruce on eskers in northeast Saskatchewan. It has been suggested that white spruce will be found on eskers if there are nearby stands of white spruce as seed sources (Argus, 1966:126).

Finally, there are lake and river margin communities distinct from the bogs and fens mentioned above. Where much alluvium has been deposited in slow moving stretches, there will be willow thickets. Alder thickets can be found on sheltered shores and around small lakes (Baldwin, 1953:120-121). Rocky edges may bear lichen growth. There is no one "typical" community; the nature of the vegetation depends on the nature of the shoreline (Ritchie, 1959:32; Argus, 1966: 126).

The Role of Forest Fires

Fire is the main agent of change acting on the mature communities described above. It maintains plant diversity by destroying vegetation, triggering a successional process (Schweger, n.d.:2). Fires are generally caused by the lightning of thunderstorms that are common in those areas of central Canada dominated by Pacific air and near frontal activity. In the Keewatin, that means south of the treeline, the summer position of the front. Fires along the front itself are few and short-lived because they get frontal rain. Unfortunately, the width of this frontal position is unknown. In territory dominated by cool, moist Arctic air north of the front there is a low incidence of fire, although those that do start may burn a long time as there is usually no rain to extinguish them (Nichols, 1967:188). Because of the relative unimportance of tundra fires, however, only the effects of fire on the Lichen-Woodland Subzone will be

considered.

Lightning-caused storms are important. For example, in Alaska they account for 75% of the area burnt (Kayll, 1968: 3). Scotter reported that in the Keewatin region, lightning started 72% of the fires on the winter range of the barren-ground caribou between 1961 and 1964 (Scotter, 1970:92). Further, the area burned by lightning fires is greater than the area burned by man-caused fires (Rowe and Scotter, 1973: 447). However, there seems to have been an increase in the total amount of fire destruction "in recent years" that seems to coincide with mining activity and white settlement (Scotter, 1970:90). Therefore the number of fires and the number of acres burned may not be representative of the aboriginal situation.

The northern coniferous forest is "peculiarly liable to destruction by fire" (Bell, 1889:1). The trees are relatively small in the Lichen-Woodland, and branches grow all the way to the ground. It was noted earlier that few trees are fire-resistant, and that most are in fact fire-adapted. Open spaces are covered with lichens that are tinder-dry and thus highly flammable in summer; many of the trees are also covered with these lichens (Bell, 1889:1).

Few fires in the Lichen-Woodland burn large areas, nevertheless. "All begin at a point, and most are still small when extinguished naturally or by man" (Rowe and Scotter, 1973:453). In Scotter's study of the winter range

of the barren-ground caribou, he found that 60% of all fires were less than 10 acres in size (Scotter, 1970:91). In northern Saskatchewan, 88% of all fires were under 100 acres (Rowe and Scotter, 1973:453). There are a few major holocausts that account for more acres burned than do the large number of small fires, but they rarely destroy a forest completely. Instead, small islands of vegetation escape. In Scotter's four-year study, no more than 2.7% of winter range was burned, and this total is probably larger than would have been the case in the aboriginal period (Scotter, 1970:91; Rowe and Scotter, 1973:453).

Archeological investigations in Lichen-Woodland and Forest-Tundra areas between Great Bear and Great Slave Lakes indicate that although fires seem to have been common, they were typically small and localized. Whether these prehistoric fires were caused by man or by lightning is undetermined (Noble, 1972:15,17,21,23).

Fire plays six important roles in affecting growing conditions:

1. It reduces competition for moisture, nutrients, heat, and light by eliminating temporarily the understory and overstory (Heinselman, 1971:64; Scotter, 1964:64).

2. By removing excessive humus it may create suitable seedbeds by exposing mineral soil where moisture and nutrient conditions are more favorable than in the thick, loose litter and humus layers of the old stands (Heinselman, 1971:64; Scotter, 1964:62,75; Kayll, 1968:Abstract).

3. Mineral elements needed for plant growth will be released. The rate of plant decay and recycling is generally slow in the cool northern forests with

their short summers, and fire more rapidly converts this humus and litter into a good supply of plant food favorable both to soil organisms and to plants growing on the soil (Heinselman, 1971:64; Scotter, 1964:73; Kayll, 1968:2,7; Fowells and Stephenson, 1934).

4. Burned areas will have higher soil temperatures than forested areas, primarily due to the addition of charcoal which absorbs heat. Also, because there is a reduced amount of unincorporated organic material to act as an insulating factor, this extra heat will act to depress the permafrost table and create a warmer environment for roots in the deeper active zone. In the winter, burned areas may be cooler than forested areas, again due to the lack of insulating material. On the other hand, snow can insulate the ground sufficiently to retain higher soil temperatures throughout the winter (Scotter, 1964:69-70; Rowe and Scotter, 1973:455-456; Kayll, 1968:7).

5. Fire may trigger the release of large numbers of seeds, especially black spruce and jackpine, or stimulate vegetative reproduction, such as aspen suckering (Heinselman, 1971:64; Kayll, 1968:4-6).

6. Fire keeps a significant percentage of each region in young stands, which are less susceptible to certain insects, to disease, and to windfall (Heinselman, 1971:64; Kayll, 1968:3,7-8). Bell described the visual effect of this latter role (1889:1): ". . . if one ascends a hill in any part of these regions . . . he will find the normal condition of the woods to be 'patchy,' or to consist of areas of second growths of various ages mixed with others of older timber."

Fires make sites generally good for new growth, but the actual plant succession depends on factors such as the nature of the fire, whether a light ground fire or an intense crown fire, and on seeds available for dispersal (Kayll, 1968:3; Scotter, 1964:57; Raup, 1935:19; Schweger, n.d.:6). Less intense fires are not too hard on shrubs, herbs, and mosses, as they destroy often only the aerial parts, not the roots. This instance is especially true for spring fires,

when the wet and frozen subsurface conditions preserve the organic horizon from even the most severe burning (Rowe and Scotter, 1973:452). Shrubs especially and mosses can regenerate vegetatively through sprouts arising from stem bases and roots. Herbs rely on their light, wind-born seed to complement the vegetative process, as do shrubs to a lesser extent (Kayll, 1968:6-7). Consequently, it is not surprising to find shrubs, herbs, and mosses among the pioneer species following a burn.

Plant Succession Following Fire

There are three general seral stages, or stages of plant succession, following a fire:

1. Young treeless or mixed community--1-10 years.
2. Young mixed forest--11-30/50 years.
3. Older mixed forest--30/50+ years.

Mosses are among the first pioneers the first spring after a fire. Grasses, herbs, and shrubs are also rapid colonizers, especially fireweed (Epilobium spp.), sedges, woodland horsetail (Equisetum sylvaticum), and willows. Tamarack, jackpine, white birch, aspen, and poplar seedings appear, with aspen producing sprouts through suckering as well. The small plants and leaves of the young deciduous trees renew the humus layer that was removed by the fire. Lichens are characterized by slow growth and a long life span, so they suffer the most after a fire, invading slowly and in small numbers. Those in this first period are

unimportant for caribou forage (Scotter, 1964:57,62-65).

In the second stage mosses are still plentiful, but grasses, grass-like plants, and herbs have become infrequent, due to shade intolerance and competition from mosses and shrubs. Most shrubs are berry-producers. Although black and white spruce are present in suitable locations, they are oyertopped by the faster-growing deciduous trees. The community is characterized by this mixed stand of trees and shrubs. Although more lichens are present, they are usually small and do not form clumps (Scotter, 1964:57-58,63; Ritchie, 1959:13; Schweger, n.d.:2).

The final and immediately sub-climax stage begins at about 50 years (about 30 years for shrubs), when mosses can now form an almost continuous carpet in suitable sites, and the discontinuous shrub layer characteristic of the climax forest is present. In this older mixed forest the long-living spruce are beginning to attain dominance as they increase in numbers and replace dying deciduous trees. Poplars attain full size and decay in about 70 years; birch show signs of old age between 50 and 75 years. Lichens recover fully in this second 50 years, with the best forage lichens mature after 120 years (Scotter, 1964:58,60,64-65; Ritchie, 1959:14; Bell, 1889:3).

To summarize, a mature spruce forest dominated by either white or black spruce is associated with good lichen growth and/or a ground cover of moss and a low degree of

plant diversity compared to earlier periods of succession, which exhibit large numbers of rapidly growing plants good for browsing and grazing. Where jackpine are prevalent, there will be good lichens but little moss. The increased litter cover that has slowly built up and the shading by the crown inhibits the latter sort of plant growth (Scotter, 1964:66; Schweger, n.d.:2). The fact that fire is beneficial to herbs, shrubs, and deciduous trees and devastating to spruce and lichens will have a decided effect on the distribution of animals in the region.

Forest-Tundra Subzone

The Forest-Tundra Subzone, or ecotone, is a combination of both tundra and forest communities, but not simply a mixing of the two adjacent zones. Tundra plant communities are floristically depauperate; that is, they contain fewer species than would be expected from examining similar communities farther north in a completely tundra environment. Therefore these communities increase in numbers of species as one goes north. This situation is more pronounced to the east, where the Ennadai Lake region was studied, than to the west, in the Artillery Lake region (Larsen, 1967:1-2; Larsen, 1971a:155,160). This difference may reflect the steeper climatic gradients and more abrupt transition found to the west (Larsen, 1971a:155).

Although the same phenomenon was expected for forest plants, a depauperate community was not encountered. There

was "no apparent change" in the total number of species associated with the spruce clumps (Larsen, 1967:11). The reasons are not obvious, except that perhaps the forest canopy sufficiently ameliorates the microclimate (Larsen, 1967:10-12). Another reason might be related to the distribution of podzol soils, associated with coniferous forests, which extend far north of the treeline to areas where forests once grew (Bryson et al., 1965; Sorenson et al., 1971). Perhaps this soil type provides an unsuitable substrate for many tundra species. Looking at the problem simplistically from a climatic point of view, one might say merely that plants that do well in the cool summer Arctic air will do less well in the warmer Pacific air, and vice versa (Larsen, 1971b: 188). Therefore it is not surprising to find tundra communities in exposed sites and forest communities in protected ones. Their association in a single subzone means that both forest and tundra animals are likely to be found here, though in smaller numbers than in the subzone to which each is primarily adapted.

D. ANIMALS

Primary Consumers: Herbivores

The green plants are the primary producers of the food chains, transforming the sun's radiant energy into vegetable life. In turn, plant-eating animals or herbivores convert some of this energy into animal tissues. They are

the primary consumers, and among terrestrial vertebrates they include members of the orders of rodents, lagomorphs, artiodactyls, and non-predatory birds. Rodents comprise a variety of usually small, gnawing mammals such as mice, lemmings, squirrels, and muskrats, as well as the larger beaver. Lagomorphs are rabbits and hares. Artiodactyls are hoofed mammals like caribou, moose, and musk-ox. Finally, non-predatory birds include many of the small birds as well as many of the traditional game birds such as grouse, ptarmigan, and ducks. For simplicity's sake in dealing with the large but mostly seasonal bird population, only the latter group, the game birds will be considered. Ducks, geese, and swans are considered here as one "type" of game bird in that they all tend to inhabit and obtain their energy from wet and aquatic environments. Actually, they are a diverse lot in that it is difficult to categorize them, ducks especially, as herbivores or predators. The same problem is true with fish, not surprising since both fish and these birds rely on aquatic systems, though only fish live exclusively in an aquatic habitat. Because of their "role" as prey to carnivores, however, it seems appropriate to include ducks, geese, swans with herbivores. There are fish that could perhaps be assigned to this category, but since fish are limited by different factors than are terrestrial or avifauna, they will be discussed separately in a later section.

Most herbivores are restricted at least seasonally

to either the Tundra or Lichen-Woodland because they are adapted to particular vegetation, and/or they have special adaptations to climatic conditions. The nature of the vegetation in each zone has several consequences for species number and distribution.

First, tundra herbivores are usually indigenous to the tundra alone, while those of the Lichen-Woodland comprise for the most part the same species found also in the Boreal Forest to the south, not surprising since the two latter subzones contain essentially the same components. The exceptions are those few species that divide their time between the two regions and the migratory birds which leave the Keewatin entirely every winter. Because characteristic forest vegetation is found right to the limit of trees, the associated fauna may also be found in suitable locales throughout the Forest-Tundra Subzone, wherever groves of trees are large enough to contain viable population units. Tundra fauna may be found to at least the southern edge of this ecotone. The Ecotone should therefore be rich in species, if poor in actual numbers of animals of each species due to the relatively smaller amounts of suitable habitats available.

A second consequence reflects the fact that the plant resources are richer and more varied in the forest than on the tundra, a less productive environment. This difference affects the number of primary consumer species found in each. Tundra species include in the summer five

rodents, one hare, two ptarmigans, a host of ducks, geese, and swans, and the musk-ox and barren-ground caribou (for details, see Chart 1).* Two of these, the caribou and willow ptarmigan, always leave the tundra in the winter to enter the shelter of the forest, while the Arctic hare and rock ptarmigan may leave if the weather is especially severe.** The migratory flocks fly completely out of the Keewatin each fall. So as few as six of the original ten species, not including the ducks, geese, and swans, may remain on the tundra all winter. Furthermore, lemming populations are cyclic in nature: they are subject to violent three- to four-year cyclic oscillations in population size and density. In the year following the population "crash"*** in their cycle, they are virtually absent on the tundra (Pitelka, 1967:153; Elton [orig. 1942], 1965; Keith, 1963:3; Soper, n.d.:25).

Forest herbivores present a picture of comparative abundance (see Chart 1). In the summer there are twelve species of rodents, one hare, three grouse, numbers of ducks, geese, and swans, and three hoofed mammals: the moose,

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*For bibliographic references used for each animal, see Appendix A).

**Although some caribou do usually winter on the tundra (Kelsall, 1968:64-65), they are in the minority and are limited in distribution. The seasonal migration into the forest seems to be the more characteristic behavioral pattern.

***Population "crashes" in these northern cycles involve a rapid decline of population in a short time, within a season or a few weeks.

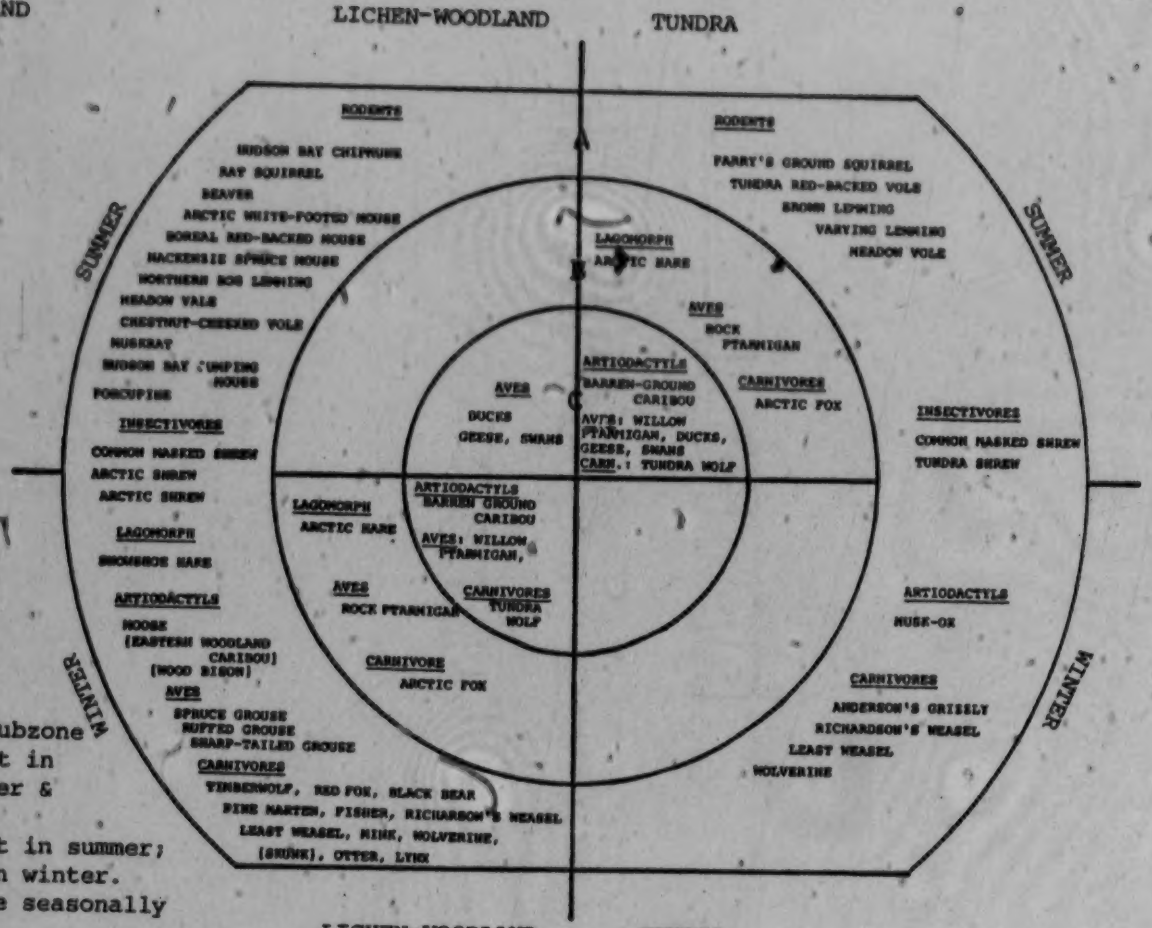
Chart 1

SPECIES DISTRIBUTION:

SHRUBBY TUNDRA AND

LICHEN-WOODLAND

SUBZONES



[ ] Marginal to Subzone

A = always present in subzone, summer & winter.

B = always present in summer; may migrate in winter.

C = always migrate seasonally

woodland caribou, and wood bison. The two latter species are marginal to the region, however, with the woodland caribou found only rarely east of the Slave River and north of the Churchill River (Parker, 1972a:16) and the bison slightly east of the Slave only to the western edge of the Shield (Hewitt, 1921:114; Preble, 1908:143). The species list of nineteen (again excluding ducks, geese, and swans) is increased in the winter with the addition of the two to four tundra species that enter the forest. The migratory birds leave the forest, however. Population cycles are three to four years for forest voles, but they are longer for larger animals, averaging nine to ten years for hares, muskrats, and grouse. These species fluctuate in synchrony, magnifying the effect. Beaver may have even longer cycles as well as possibly moose and barren-ground caribou (Hewitt, 1921:216; Keith, 1963:29,43,67; Fuller, 1967:182).

The nature of the vegetation affects also the pattern of distribution of herbivores within each zone. Tundra vegetation is characterized by an interdigitation of plant communities, with a corresponding mixed pattern of animal distribution and no large zones restricting animal location. Per contra, forest species can be divided into two spatially distinct configurations based on the nature of the plant communities on which they depend. Fire was defined earlier as the factor that initiates a sequence of plant succession culminating in a long-lived "climax" vegetation, thus

dividing plant communities into successional or climax types. Because fires are limited largely to the forest, this phenomenon is generally absent from the tundra and has not been discussed for that zone. Some plant communities along the edges of lakes and waterways and in fens may be considered analogous to successional communities in that they contain many of the same sorts of species introduced after a fire, especially willows and grass-like plants. The animal configurations can be drawn around the two important forest hoofed mamals, the barren-ground caribou and the moose, each utilizing and adapting to climax and subclimax vegetation respectively. The annual cycle of each will be described to distinguish them, then the other herbivores can be divided into corresponding groupings.

The Barren-Ground Caribou Annual Cycle

The caribou annual cycle of movement has been fairly well studied, especially by Banfield (1951b), Kelsall (1968), and Parker (1972a). From late April to early June caribou move from their winter ranges in the Lichen-Woodland Subzone to calving grounds for females and summer ranges for both females and males (Kelsall, 1968:143; Parker, 1972a:24-26). Their spring migration routes lie along waterways where they can cross on frozen lakes and rivers (Banfield, 1951b:9; Kelsall, 1968:116). They travel also on eskers, which are wind-swept of snow when the lower land is still deeply covered and also when it is wet with spring thaw. Some

eskers extend from the forest far onto the tundra, providing easy access between the two areas (Kelsall, 1968:58-59).

The breeding cows end their migration in June in high, rough country, where they calve between June 10-15. Then they and their young move to the nearest rich pasture. Such pasture may be as far north as the coastal plains or the rich vegetation along major lake and river valleys (Kelsall, 1968: 106). The males travel shorter distances than do the females, meeting them when the cows start moving inland again at the end of July. There is then a mid-summer southern migration that terminates in mid-August (Pike, 1892:46; Parker, 1972a: 34-38).

During July and often early August the caribou are both nomadic and gregarious. Three factors seem to determine their movements (Kelsall, 1968:106-107).

1. The intensity and type of insect harassment;
2. The direction and duration of winds; and
3. The need to find good pastures.

They will often resort to the wind-swept eskers again, this time for refuge from flies and mosquitos (Kelsall, 1968:58). During the summer period they generally wander back toward their winter ranges. Huge aggregations will form at water barriers, disperse again into small groups and individuals over wide areas once the barrier is passed (Kelsall, 1968: 107; Banfield, 1951b:4). As insects become less bothersome in August, the large concentrations of animals break up, dispersing themselves over much of their summer range

(Parker, 1972a:40).

By late August and into September the caribou reach the treeline and move along its edge, again gathering into large herds (Kelsall, 1968:59,107; Banfield, 1951b:4). They may enter the forest briefly in two places: the Snare River watershed between Great Bear and Great Slave Lakes and the Duck Lake (Nijanilini) area in northern Manitoba. Since the fly season has ended, the caribou can feed intensively as they travel leisurely, building up fat reserves for the fall rut and migration (Kelsall, 1968:107).

The rut occurs in late October, while the caribou are still in the treeline area. The fall migration may have already started. The caribou will follow the heights of land and cross the waterways, a change from their spring pattern when lakes and streams were still frozen. Now lakes and river systems provide barriers which must be detoured or swum. When the barrier is small, swimming is easy, but larger water obstacles cause "bunching" and movement to easily forded narrows. Many of these crossings are predictable, and caribou can be expected to use them every fall (Kelsall, 1968:58; Harp, 1961:47; Parker, 1972a:43-45).

Fall migration is completed usually by early November or late December, with most animals reaching their wintering areas in the Lichen-Woodland Subzone by early December. Males move farther south into the forest than do females (Parker, 1972a:52). The caribou move within this winter

territory according to pasture and weather conditions, feeding primarily on lichens in mature coniferous forest. The best winter range is in a belt within 100 miles of the treeline (Thomas, 1969:17), which possibly is the same area that receives more rain in the summer and thus has less extensive fires.

From February to April the caribou become restless and start to drift toward the treeline, gathering into large, loose aggregations in preparation for the spring migration (Kelsall, 1968:107). The annual cycle then repeats itself. Historical accounts reviewed by Parker (1972a) suggest that seasonal movements and distribution were very similar in the early eighteenth century to those which exist today, at least for the Kaminuriak population, the easternmost group of caribou in the Keewatin.

This cycle is characteristic for the three caribou populations in the study area: the Kaminuriak, the Beverly, and the Bathurst populations. The names refer to their usual calving areas on the tundra. The populations tend to be discrete, with little mixing of animals except perhaps when winter ranges overlap. The Kaminuriak population winters usually from northern Manitoba to northeastern Saskatchewan; the Beverly from northeastern Saskatchewan to the northeast arm of Great Slave Lake; and the Bathurst group from Great Slave Lake to Great Bear Lake (Thomas, 1969:7-17).

Factors Determining Caribou Movement and Distribution

Although there are favorite calving grounds, migration

routes, and wintering ranges, caribou may change their routes and ranges annually. Such changes may involve broad, lateral shifts across their regular line of movement, changing composition of herds in size and membership, and irregular use of a range (Kelsall, 1968:108; Parker, 1972a; Burch, 1972:351-352). Further, there are always some animals that winter on the tundra, increasing in number during mild winters (Kelsall, 1968:64-65). Caribou are rarely distributed evenly. Usually a winter range has a few small areas with abundant caribou, larger areas where they are thinly spread, and still others where there are none at all. Their distribution changes continually due to weather and food conditions (Kelsall, 1968:136; Banfield, 1951b:7; Parker, 1972a:10,48; Pruitt, 1959:163).

There are three factors determining caribou movements to and within various locales. Wind seems to be a prime factor. Kelsall discovered that caribou do not always head into the wind, a common northern belief (cf. Hearne [orig. 1795], 1958:127; Franklin [orig. 1823], 1969:242). The caribou do head into the wind in summer, and they also seek out windy spots for resting places during the fly season. When temperatures drop, however, and insects are no longer a problem, they will drift with the wind. During migration itself, only winds over gale speeds (32 MPH) will affect their movement. Because the windchill is almost always greater on the treeless tundra than in the forest, they will

tend to seek shelter in the woods. Again, on mild, windless days they may move onto the edge of the tundra.

The second important factor affecting their distribution and movement is snow conditions. Snow may affect migration. Kelsall found that in their spring migration caribou usually passed through an area 2-1/2 to 3 weeks before the mean date for last snow cover in that area, although there is not necessarily a causal factor involved (Kelsall, 1968:117). Possibly fall migration is triggered by the first "substantial" snowfall (Kelsall, 1968:113).

Caribou avoid both deep, wind-packed snow and heavily-crusted snow (Kelsall, 1968:65) because they have trouble digging through to obtain food. On the tundra snow tends to drift into low elevations such as river valleys and lake margins, which are also the richest in vegetation. The great depths of packed snow make this vegetation largely inaccessible. In the forest snow is less wind-blown and therefore remains softer. Although the mean annual total snowfall on caribou range is 76.9 to 128.2 cm. (30 to 50 inches), the mean annual maximum depth is only between 51.2 and 76.9 cm. (20 and 30 inches). Caribou have few problems feeding or traveling in snow depths of less than 58.9 cm. (23 inches), and they will seek out these conditions, avoiding snow depths greater than 60.0 cm. (a little less than two feet). In a winter with less snow than average, caribou will therefore need to move less and will be more stationary, dispersing over a relatively wide area. Winters with considerable snow

will see caribou continuing to travel in tighter herds until more favorable snow depths are found (Parker, 1972a:48; Kelsall, 1968:47-48; Pruitt, 1959:165-167,170).

If snowfall were especially severe, over 50 cm. (20.8 inches) deep at densities of 0.30 or greater, the caribou population could decline rapidly over the course of one winter due to starvation. A too-early thaw or rain could have the same effect if it were followed by a freeze, forming an icy crust over the snow thick enough to keep the caribou from feeding (Kelsall, 1968:70).

The third main factor determining caribou movement is suitable pasture. Lichens and other plant foods to which the caribou is adapted grow slowly in northern climates. Possibly caribou shift their range every ten years or so, other factors being equal, which would allow the pasture to recover (Kelsall, 1968:120). More drastic shifts are caused by burned areas. A large burn will deflect the path of a migration in the same way as will a topographical barrier for two reasons: first, a burn lacks lichen components. Over twenty years are necessary to regrow enough vegetation for adequate grazing, and at least seventy-five years are required for the lichen growth to provide really good forage. A large burn could significantly reduce possible range, especially in an area favored by caribou. The second reason for avoidance of those areas by caribou may be that snow and wind conditions in large burns may be similar to those on

the exposed tundra, both a significant windchill factor and snow too deep and/or hard to meet caribou requirements (Kelsall, 1968:263,267,294; Scotter, 1964:37; Leopold and Darling, 1953:554). Therefore caribou wintering in the Lichen-Woodland Subzone are restricted mainly to mature coniferous forests containing lichens.

The Moose Annual Cycle

Moose differ greatly from caribou in their habits. They are relatively solitary and non-migratory, and they eat an entirely different type of vegetation. Generally they range within the treeline, but they have on occasion been found far out on the tundra, where they can eat willows in the draws (Leopold and Darling, 1953:553; Peterson, 1955: 42-43). Their northern range within the forest has been increasing since perhaps 1875 or at least the turn of the century (Peterson, 1955:16; Mercer and Kitchen, 1968:62). Quite possibly they were rare to absent, and certainly they were uncommon before that period in the Lichen-Woodland Subzone. Samuel Hearne saw no moose on his travels through the area except south of Great Slave Lake, and he was quite explicit in stating that moose "are never found in the Northern Indian territories" (Hearne [orig. 1795], 1958: 135).*

*Although Hearne noted this observation before he had traveled extensively in the forest, he did not later modify it except in reference to the area south of Great Slave Lake, so it can be assumed he meant it as it is written.

Moose are not migratory, but they will make seasonal shifts from one locale to another in response to changes in seasonal food supply. In the spring, moose tend to concentrate around lakes and streams to eat aquatic vegetation such as pond-weeds, water lilies, and the vegetation in early seral stages on its fringes: sedges, grasses, twigs of willow and aspen (Peterson, 1955:110,116; Shelford and Olson, 1935:384). They may also chew bark from trees when the sap is rising, before the trees leaf out (Peterson, 1955:114). Aquatic and semi-aquatic plants are used throughout the summer, declining in importance in late summer when they become less palatable (Peterson, 1955:119).

The beginning of freeze-up forces moose away from their marshy habitat into drier conditions, where they feed until spring on willows, aspen, herbaceous growths, shrubs, and other small deciduous trees such as birch (Shelford and Olson, 1935:384; Spencer and Chatelain, 1953:542). These plant foods are typical subclimax species found in areas that have been flooded (naturally or by beaver intervention) or burned (Spencer and Chatelain, 1953:541; Leopold and Darling, 1953:553). So although moose may shelter in climax forest, they can use only those areas of climax vegetation where the climax is broken and discontinuous, providing them with suitable forage.

The basis of good winter moose habitat, therefore, is continual forest succession. A moose population will reach

its maximum number in early stages of succession. Good aspen browse (through suckering) is available within two to three years, and within five years, black spruce, birch, willow, and aspen seedlings will show high density, though they may not reach above the snowline (Spencer and Chatelain, 1953:546; Peterson, 1955:153). Good forage is available for fifteen to twenty years if there are moose in the area to eat it and keep it down. Otherwise, it will all grow out of reach within a few years, creating a dense closed canopy with little understory, eventually being replaced by a climax growth (Spencer and Chatelain, 1953:545-546; Peterson, 1955:164). Because of their seasonal shifts, moose need both good summer and winter habitat to support a sizeable population.

Forest Herbivore Configurations

For the most part, barren-ground caribou and moose occupy complementaty and discrete habitats. If one is present, the other will likely be absent. Fire contributes to winter habitat for moose, but it destroys the lichens on which the caribou depend at that season. Clearing of the forest by other means could have the same effect Leopold and Darling, 1953:554-555).

Many of the other herbivores living in the Lichen-Woodland are similarly restricted. The red squirrel, spruce grouse, and woodland caribou all live in climax coniferous forest, as do the red-backed vole and the Mackenzie spruce mouse. The two latter species live also in other plant

communities, but none specifically successional. Living primarily in successional plant communities are the snowshoe hare, the sharp-tailed and ruffed grouse, and marginally, in the Slave River area, the Hudson Bay chipmunk and the wood bison (which depends also on prairie habitats). Beaver, muskrat, ducks, geese, and swans occupy the moose's summer habitat, at least the aquatic portion. Successional vegetation is beneficial to muskrats and beaver. A region could support at least small populations of this last group yet have few moose if the suitable winter habitat were not available.

Secondary Consumers: Predators

The primary consumers form the usual diet of meat-eating animals. As in any food chain, the number of animals decreases at a higher tropical level: there are always more primary than secondary consumers. Such secondary consumers include carnivores such as wolves, otters, and lynx, among others, and raptorial birds, or birds of prey. Insectivores are a special type of predator, in that they rely not only on small herbivores but also on insects. Further, they are often eaten by larger carnivores along with rodents. Raptorial birds will not be considered, although they are significant predators. They are not important as food for other species or for their hides, which militates against their inclusion.

The summary inventory of tundra carnivores (see

Chart 1) is even shorter than that of the herbivores: there are two shrews and six carnivores: the tundra wolf, Arctic fox, Anderson's grizzly (actually an omnivore), Richardson's weasel, least weasel, and wolverine. Of these, the wolf migrates each fall into the forest following the caribou, and the Arctic fox may migrate depending on the difficulty in obtaining food. Its main prey, the lemmings, cycle every three to four years, and following their "crash" it may look elsewhere for food. Also, in the winter many of the rodents do not occupy their roles as "prey" because they are buried under a hard, protective snow crust through which it is difficult for a predator to dig. A search for easier prey to obtain might induce the fox to move into the softer snow of the forest. However, foxes that migrate would probably perish since they are not adapted for the soft, deep forest-snow; it would thus be a one-way migration.

In the forest there are three shrews, including a sub-species of one found on the tundra, and twelve carnivores: the timber wolf, red fox, black bear, pine marten, fisher, Richardson's weasel, least weasel, wolverine, otter, mink, lynx, and skunk (marginal to the area, found only in the Slave River region). Their numbers increase by one to two species in the winter. Coyotes can be found in the region now, but they were not likely present in pre-contact times, so they are not included in the discussion.

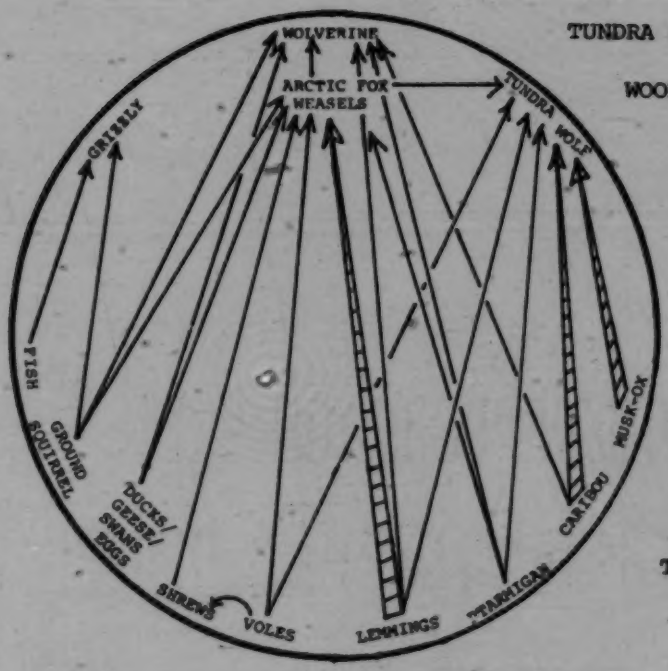
Predator-Prey Relationships

There are both distinct and generalized predator-prey relationships (see Chart 2). On the tundra the Arctic fox expecially and the Richardson's weasel are linked to the two lemming genera, with tundra wolves the only animals that will seriously harass barren-ground caribou and musk-ox. Special relationships exist in the forest between red squirrels and marten; hares and lynx; muskrat/beaver (fish) and mink/otter; and caribou/moose and wolves. This more specialized predation pattern is partly revealed in the three to four year cycle of the tundra carnivores (Hewitt, 1921:228; Keith, 1963:47; Elton, 1965:272,448; Harper, 1956:66) and in the nine to ten year cycle of the lynx and mink (Keith, 1963:44-46,50,67; Elton, 1921:219-220,230; Preble, 1908:209; Soper, n.d.:40). Red fox and marten also cycle every nine to ten years (Fuller, 1971:182). Predators are affected by the cycling of their prey to the degree that they tend toward a one-to-one relationship with them.

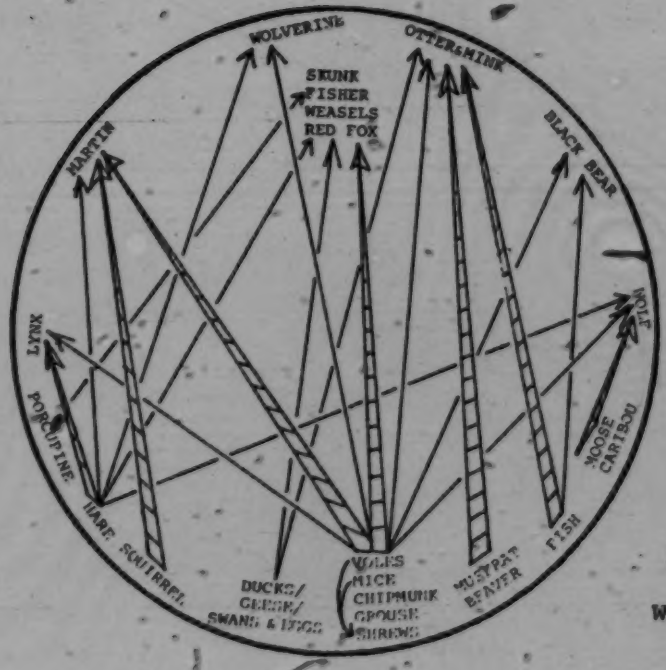
Such specialization of predators means that they tend to be restricted, like herbivores, to particular types of plant communities. This statement is an over-simplification of the actual situation, in that most animals use more than one plant community. Since there do seem to be some significant links in the food web, however, the predators can be tentatively grouped with the species they tend to prey on. Tundra wolves and marten thus can be added to the list of

CHART 2

TUNDRA & LICHEN-WOODLAND FOOD WEBS



TUNDRA



LICHEN-WOODLAND

animals living in climax communities; lynx and timber wolves are found expecially in successional communities; mink and otter are found in rivers, lakes, and fen-type environments. The black bear is actually an omnivore that prefers the sub-climax for the greater variety of plant and animal foods to be found there. Other carnivores hunt in both locales, as will those listed above should the opportunity present itself.

To conclude, fire plays a major role in determining the clusters of animals that live in the Lichen-Woodland Subzone. Frequent burning would likely lead to an influx of moose into the region as well as open up more habitat for smaller herbivores and, indirectly, their predators. Further, fires act to diversify environments. Because animals do utilize multiple habitats, fires should "increase the diversity of the fauna as well as the population density of some species" (Rowe and Scotter, 1973:458). However, carrying capacity of suitable habitat for caribou appears to be greater than that for moose (Scotter, 1964:78), probably because caribou spend only part of their year in the forest. It would be disadvantageous for a human population dependent upon large herbivores for a good part of their diet to burn off vegetation indiscriminately. Selective burning could increase both moose and caribou pasture, however. Any burning leads to the successional vegetation that moose rely on, although on the Shield ". . . suitable browse is seldom abundant following forest fires" (Rowe and Scotter, 1973:458).

Burning the thick carpet of bryophytes found in forests and in muskegs might permit successful lichen growth, and in the short run it would create a more productive habitat (Rowe and Scotter, 1973:458). Therefore there might be a role for human manipulation of the environment on both short-term and long-term bases.

Fish

Fish are the last faunal form to be discussed. Unfortunately there is relatively little information on fish in this region. Most research has been done on the larger lakes currently used for commercial fishing, with virtually none conducted in the winter. Therefore little is known about fish in small lakes and less about winter fish conditions in any of them.

Factors affecting fish distribution and abundance are related to physiography and climate. To begin with, all the fish now in the Keewatin had to have been able to migrate into the area along waterways established since the end of glaciation. That means that the same species will probably be found along the length of such waterways or where it can be shown that they were once connected, as by a large post-glacial lake. This assumption is based on a prior one: that underwater flora, in particular plankton, the base of the food chain, will be similar in the three subzones since it is subject only to the temperature aspect of the climate. Fish whose expansion into the region was blocked in some fashion will be found only on the fringes, such as the

inconnu (Stenodus leucichthys nelma), which is distributed in the Mackenzie River system as far south as the rapids at Fort Smith, beyond which it cannot go (McPhail and Lindsey, 1970:76). There are also fish that have simply reached the limits of their ranges, however. Therefore fish species are not necessarily restricted to either tundra or forest but may be found in both.

Secondly, northern lakes in both zones are typically oligotrophic or poorly nourished, with clear, cold water and deep light penetration. Oxygen does not get used up rapidly, and there is little chance of an oxygen shortage that might lead to bottom stagnation, at least in deep lakes (Rawson, 1947:53; Rawson, 1959:15,18; Wynne-Edwards, 1952:4). There are also many stagnant ponds, however, with no outlets. Unless their depths exceed two meters, they will probably freeze to the bottom in the winter. If they have no outlets, they could not be repopulated annually from neighboring lakes or streams, and so they are not likely to contain fish. Tundra ponds are often of this type (Harper, 1948:154; Wynne-Edwards, 1952:4).

The size of the body of water is also important. Other things being equal, production of food sources for fish is a function of surface area, not of volume or depth. Further, the most productive part of any lake is the shoal-water zone near the shore. Small lakes have more shoreline in proportion to their areas than do large ones (Rostland, 1952:46), and large lakes on the Shield are characterized by very high shore developments, "the relation of actual shore

length to the minimum outline that would enclose an area equal to that of the lake" (Rawson, 1959:10). Small streams are probably more productive per unit area than large ones, and lakes more than rivers (Rostlund, 1952:46-47).

Finally, this large amount of "growing space" is offset by two specific climatic effects. First, winter lasts from freeze-up to break-up under the water, longer than to the beginning of thaw. Therefore the growing season is shorter than for terrestial plants (Rostlund, 1952:68; Wynne-Edwards, 1952:3). This factor is compensated for somewhat by the long hours of daylight in the summer. In this regard, the date of break-up is a critical point in that the earlier it occurs, the more hours of radiant energy there are for aquatic systems. Consequently, forest aquatic systems should be richer than those of the tundra. The second effect is that the typically low temperatures, again especially on the tundra, will retard growth and development, although some species have adapted so as to grow faster at lower temperatures. Such species include the whitefish (Coregonus clupeaformis, C. nasus, Prosopium cylindraceum), cisco (C. artedii), and pike (Esox lucius), though not the lake trout (Salvelinus namaycush) (Wynne-Edwards, 1952:2-3; Rostlund, 1952:68).

The fish food chain begins with the phytoplankton contained in lakes. The number of fish therefore depends on the amount of plankton available, among other factors.

Despite the counter-balances to the cold climate, plankton in the Keewatin is generally small in quantity, reflecting the harsh climatic and usually oligotrophic conditions (Rawson, 1947:54; Rostlund, 1952:44). The bottom fauna such as crustaceans, molluscs, and insect larvae that live in the ooze of lake or river bottoms are similarly affected, since they are linked to plankton detritus in their food chains (Rawson, 1947:54; Rawson, 1951:238).* The other major food source is terrestrial insects, available only in summer, though then in large quantity. This relatively small resource base is reflected in the decreasing yield of fish as one goes northward: in Lake Athabasca, 1.5 pounds of fish per acre were taken; in Great Slave Lake, 0.75 - 1.00; and in Great Bear Lake, 0.27 (Rostlund, 1952:47,68). These differences reflect also differences in amount of nutritive materials and the increasingly colder conditions to the north. Northern fish do tend to use their resources with considerable efficiency, however (Rawson, 1947:53).

There are twenty-nine species of fish representing fourteen families in the study area (see Table 1). Of these, five are actually so peripheral that they can be omitted. Eleven are marginal species, found in only part of the study area, especially in part of the Mackenzie River system and to a lesser extent in the Churchill River system. Finally, there are thirteen species distributed widely throughout the

*Since fish living in rivers have little plankton on which to rely, their food chain begins with other forms of non-floating algae and these bottom organisms.

Table 1

KEEWATIN FISH

Peripheral (5)

Lake sturgeon (Acipenser fulvescens)
Broad whitefish (Coregonus nasus)
Arctic char (Salvelinus alpinus)
Chum salmon (Oncorhynchus keta)
Fathead minnow (Pimephales promelas)

Marginal (11)

Arctic lamprey (Lampetra japonica)
Goldeye (Hiodon alosoides)
Inconnu (Stenodus leucichthys nelma)
Northern pearl dace (Semotilus margarita nachtriebi)
Fathead chub (Platygobio gracilis)
Emerald shiner (Notropis atherinoides)
Spottail shiner (Notropis hudsonius)
White sucker (Catostomus commersoni)
Trout-perch (Percopis omiscomaycus)
American yellow perch (Perca fluviatilis flavescens)
Yellow walleye (Stizostedion vitreum vitreum)

Widespread (13)

Humpback whitefish (Coregonus clupeaformis)
Lake cisco (Coregonus artedii)
Round whitefish (Prosopium cylindraceum)
Arctic grayling (Thymallus arcticus)
Lake trout (Salvelinus namaycush)
Northern pike (Esox lucius)
Lake club (Couesius plumbeus)
Longnose sucker (Catostomus catostomus)
Burbot (Lota lota)
Ninespine stickleback (Pungitius pungitius)
Deepwater sculpin (Myoxocephalus quadricornis thompsoni)
Slimy sculpin (Cottus cognatus)
Spoonhead sculpin (Cottus ricei)

region.

Among both the marginal and widespread populations, the most significant fish are the main plankton feeder, the cisco; the main bottom feeder, the humpback or common whitefish; and the main piscivorous or carnivorous species, the lake trout (Rawson, 1947:55; Rawson, 1951:211-212). These typically form part of a distinct offshore association of fish found in waters from abut 10 to 45 meters deep (33 - 150 feet), so depth too affects abundance of fish species. Long nose suckers, burbot, and sculpins are also deep water fish (Rawson, 1951:238; Rawson, 1959:29-30). Ciscoes and sculpins are important "forage fish," those eaten by other fish.

Inshore associations are quite distinct, especially along rocky shores where great depths are encountered not far out, strictly limiting this shallow zone. Typical species include pike, grayling, white sucker, perch, goldeye, and all the small or forage fish except the sculpins and ciscoes. The young of most of the larger species live in this zone, which is generally under 10 meters (33 feet) (Rawson, 1951:238; Rawson, 1959:29).

A partial, simplified food chain for Great Slave Lake

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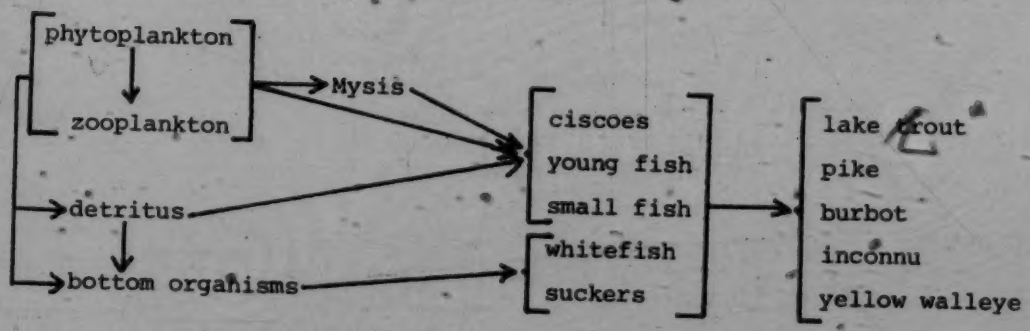
*For specific information on these species see McPhail and Lindsey, 1970; Wynne-Edwards, 1952; Rawson, 1947; Rawson, 1951; Rawson, 1959; Rostlund, 1952; Harper, 1948; Harper and Nichols, 1919; Fowler, 1948; Richardson, 1836; Hornby, 1934; Preble, 1908.

would probably be characteristic for most of the Keewatin, subtracting the fish not widely encountered. It is graphically represented in Chart 3.

CHART 3

FISH FOOD CHAIN (Rawson, 1951:238)



Fish are in turn prey to some birds and mammals. For example, in the forest they are an important prey for mink and otter as well as for bears and some raptorial birds.

Fish are a significant resource on two counts: first, because there are likely to be fish everywhere there are suitable aquatic habitats in both forest and tundra areas; their distribution cross-cuts that of the terrestrial and avifauna. Secondly, there are a lot of fish in the Keewatin simply because there are so many lakes and rivers. Even disallowing a large percentage for stagnant, shallow ponds with no fish, with water covering 10 - 20% or more of the land, there is still a lot of surface covered with water that is probably suitable.

CHAPTER 3

THE HUMAN POPULATION

From the above description of Keewatin ecosystems, the question to be answered in this section is how its elements can be used to hypothesize a niche* for humans. The first step in the ecological procedure, that of ecosystem description, has been completed; the second step involves the examination of human adaptation. Julian Steward's superficial inquiry into aboriginal Chipewyan social organization was an early effort in this direction. Harvey Feit attempted this analysis for the Mistassini Indians of eastern Canada when he set out "to reconstruct the pre-contact strategy of adaptation" (1969:Abstract) based on a description, much like the preceding one, of the boreal forest ecosystem. What he actually accomplished is recapitulated in the description of Keewatin ecosystems, for he shows only the different resources available to a human population at different stages of a successional cycle characteristic of his forest system initiated periodically by fire. He does not show an adaptive strategy, unless one assumes that the human inhabitants would either remain within a burned area for the entire successional cycle or would reinhabit the area during an early development stage. Given the probability of starvation during the first few years, the former is a dubious proposition, and there is

*A niche is not only where something lives, but also what it does there in order to survive (Odum, 1971:234).

no good reason for postulating the latter.

I would now like to move one step further and use this description to hypothesize a possible adaptive strategy for the aboriginal human inhabitants. The argument I shall use is basically that because humans in the Keewatin must depend upon relatively small, and to an extent, mutually exclusive constellations of resources, the pattern of their use is predictable or can be hypothesized. As stated in the introduction, the underlying assumption concerning the human population is that it was not altering its environment significantly. As hunters and gatherers with a relatively simple lithic-bone technology, their influence on their habitat would be minimal. The only possible exception might be deliberate, extensive burning. The effects of man-made fires can not at this time be determined, and there are no data yet on burning practices of historic populations in the area.

Furthermore, we may assume that the aboriginal inhabitants would have acted as carnivores and predators. Humans are inherently omnivorous, seeking out both plant and animal foods. Suitable vegetable resources are scant in the Keewatin, because human digestive systems are not adaptable to eating most of the vegetation that sustains the usual herbivores, especially vegetation found in winter.

Stands of seed-bearing grasses are not typical, nor are the nutritious tuberous roots which are found in more temperate regions. Some roots and lower stems of aquatic

plants are edible, and some lichens can be used for food if they are boiled into a filling if unsustaining broth (Mackenzie [orig. 1801], 1966:cxxvii). Probably the best vegetable source for humans would be berries, which are available mainly in the late summer and fall, though some species, such as cranberry (Vaccinium vitis-idaea), do keep their berries throughout the winter. Although berries could be stored through drying, they are not a protein-rich source of food. Therefore one may assume that people living at a hunting-gathering level of technology in the Keewatin could not have depended on plant foods to any substantial degree. Instead, they would have been almost wholly dependent upon animal resources--mammals, birds, and fish--for the bulk of their diet. This conclusion is supported by ethnohistorical evidence.

Available Options

There are two factors which may be considered prior to evaluating how the animal resources could have been used: the first is the concept of technoenvironmental advantage; the second, the concept of redundancy.

Technoenvironmental advantage refers to the ability of a group of people to maximize energy returns in terms of energy expenditure in the food quest. The ratio of calorie production to calorie expenditure in obtaining food must be greater than one (1.00) for a group to survive, and the ratio should increase as the exploitation of the environment

becomes more efficient (Harris, 1971:203-217).

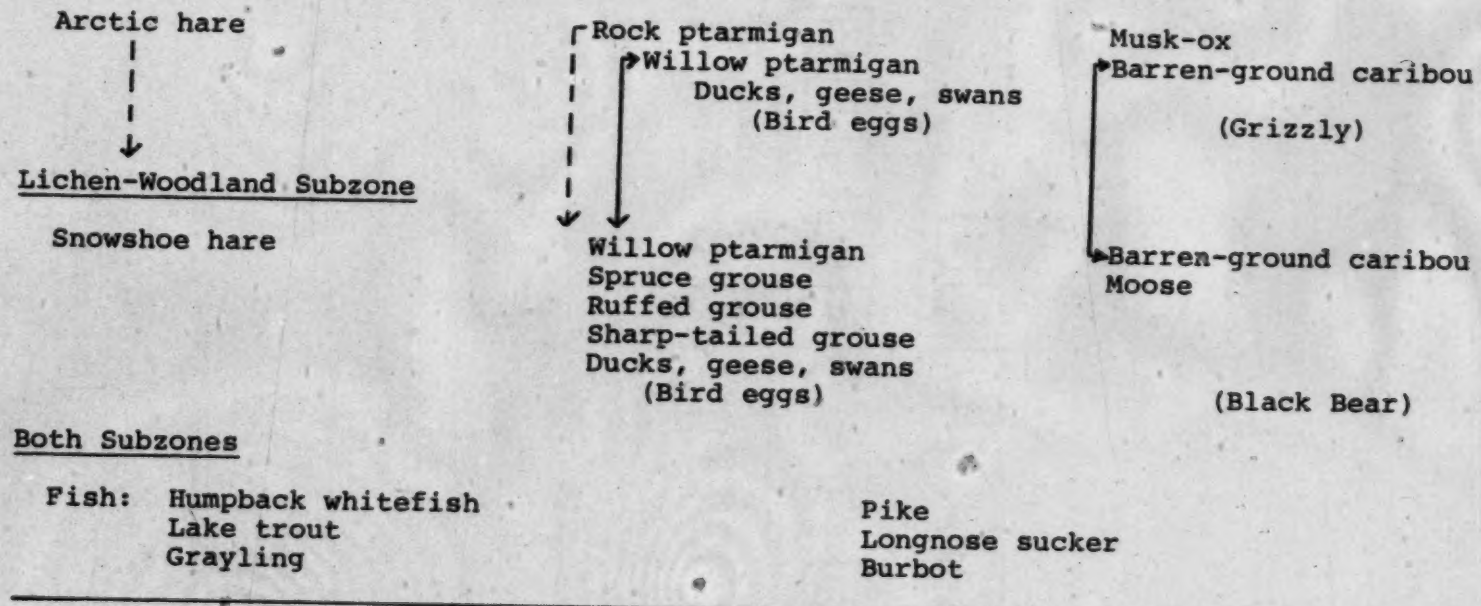
The implication of the concept for Keewatin inhabitants is that not all animals would have been equally desirable as a food or energy source. Animals difficult to hunt would have to have yielded large quantities of meat, while small animals would have to have been easily caught to warrant seeking them. Therefore carnivores, usually small, hard to catch, and fewer in number than herbivores, would not likely be desired prey, with the possible exception of black bears and grizzlies. Instead, it would have been to human advantage to have concentrated on the animals that turn the plant food into meat, the herbivores. Despite the fact that small animals such as mice generally have higher total biomass than larger ones, they would likely not be worthwhile prey. The same could be said for any animal smaller than a rabbit or a grouse, if there were a choice of prey.

If one eliminates these smaller animals, and if one eliminates those species marginal to the area, such as the woodland caribou, wood bison, and several fish, several important species are left which are depicted in Table 2. Their distribution is represented graphically in Chart 4.

There is a limited number of possibilities or options for exploiting various species by a human population which could be based on the following animals: on the tundra, the musk-ox, caribou (summer only), small game, and fish; in the forest, moose, caribou (winter only), small game, and fish. The category "small game" includes the smaller mammals and birds

Table 2

SUITABLE KEEWATIN PREY SPECIES

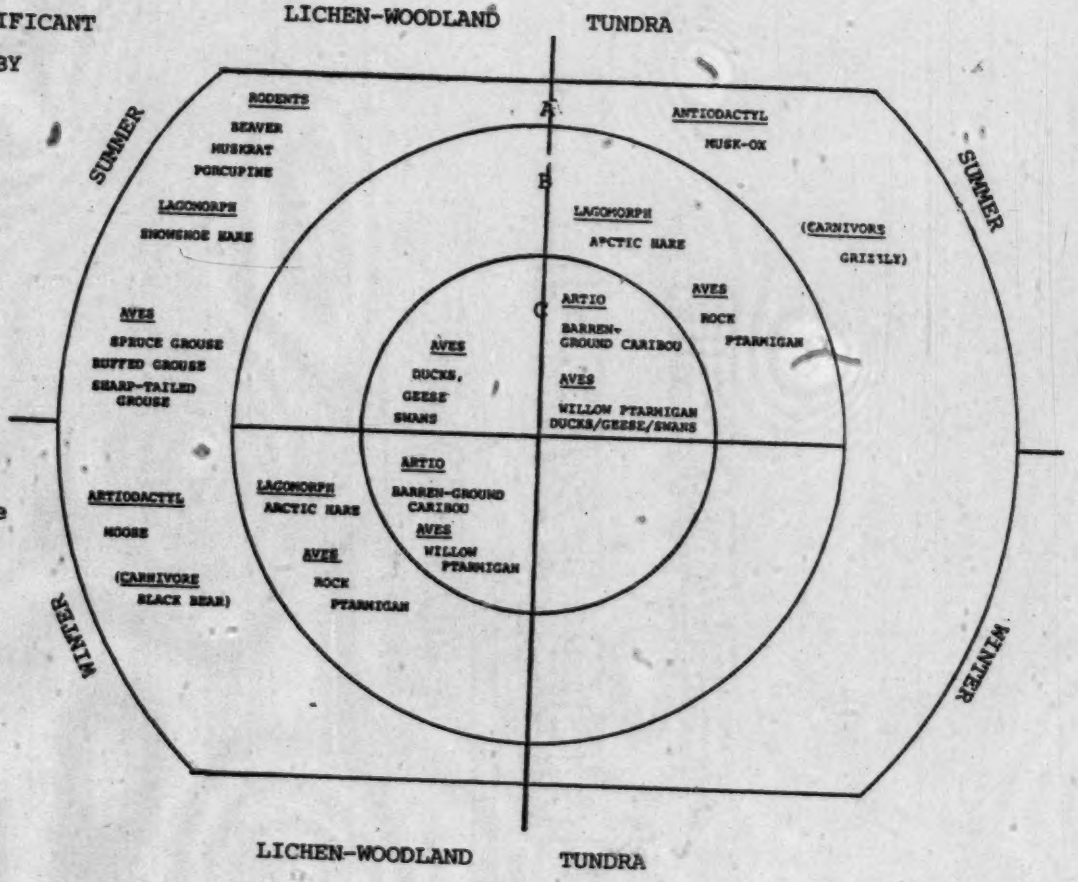


- - → may migrate to the forest in winter, though insignificant in numbers and distance

——→ always migrate between tundra and forest

Chart 4

DISTRIBUTION OF SIGNIFICANT PREY SPECIES: SHRUBBY TUNDRA AND LICHEN-WOODLAND SUBZONES



A = present in subzone year-round
B = may migrate in winter
C = always migrates seasonally

listed above, although it could be expanded to include some of the still smaller animals that were eliminated from consideration. The number of species comprising the small game category changes from summer to winter as indicated in Charts 1 and 4 .

The various combinations of the animal resources available which comprise the hunting and fishing options are listed in Table 3. Based strictly on the number of possible combinations, the number for the tundra is fifteen in the summer and seven in the winter, while in the forest they are opposite, with seven in the summer and fifteen in the winter (see Table 4).

This list can be reduced in several ways. First, small game is often less available on the tundra in the winter due to migration out of the zone or to animals being buried under a protective snow crust. The four winter options that include small game (#3,5,6,7,) could be disallowed for the tundra, making the total number of winter options only three (see Table 5).

Here the concept of redundancy may have application. By redundancy is meant ". . . alternative pathways for survival" (Alland, 1967:126). A food chain is considered tenuous and fragile when the loss of one of its links could cause the death of those species depending on it, whereas the loss of a link would be less threatening if there were alternate options. Redundancy makes possible "a certain

Table 3

ANIMAL OPTIONS AVAILABLE TO HUMANS:
SHRUBBY TUNDRA AND LICHEN-WOODLAND SUBZONES

Shrubby Tundra

Summer Options	Winter Options
*1 Musk-ox	*1 Musk-ox
*2 Fish	*2 Fish
*3 Small game	*3 Small game
*4 Caribou	4 Musk-ox & fish
5 Musk-ox & fish	*5 Musk-ox & small game
6 Musk-ox & small game	*6 Musk-ox, fish, & small game
7 Musk-ox, fish, & small game	*7 Fish & small game
8 Musk-ox & caribou	
9 Caribou & fish	
10 Caribou & small game	
11 Caribou, fish, & small game	
12 Caribou, musk-ox & fish	
13 Caribou, musk-ox & small game	
14 Caribou, musk-ox, fish, & small game	
15 Fish & small game	

Lichen-Woodland

Summer Options	Winter Options
*1 Moose	*1 Moose
*2 Fish	*2 Fish
*3 Small game	*3 Small game
4 Moose & fish	*4 Caribou
5 Moose & small game	5 Moose & fish
6 Moose, fish, & small game	6 Moose & small game
7 Fish & small game	7 Moose, fish, & small game
	8 Moose & caribou
	9 Caribou & fish
	10 Caribou & small game
	11 Caribou, fish, & small game
	12 Caribou, moose, & fish
	13 Caribou, moose, & small game
	14 Caribou, moose, fish, & small game
	15 Fish & small game

* = eliminated option (see text)

Table 4

NUMBERS OF ANIMAL OPTIONS

Season	Summer	Winter
Zone		
Tundra	15	7
Forest	7	15

Table 5

REVISION #1: NUMBERS OF ANIMAL OPTIONS

Season	Summer	Winter
Zone		
Tundra	15	3
Forest	7	15

stability for the system under stress . . . a greater differentiation of parts has the added advantage of storing potential variation which can be exploited in different ways if the environmental situation is changed in some way (Alland, 1967:126). The technoenvironmental advantage of a total exploitative system may be predicated upon such redundancy.

Burch expresses a similar idea with an emphasis on scarce resources. He feels that if periods of scarcity are frequent, as in the Keewatin, effective alternative responses are likely to be built into the normal way of life, that is, into the annual cycle, of the human populations concerned. It is an alternate pattern that is regularly put into operation as soon as the existence of, or potential for, a crisis is perceived (Burch, 1972:255).

Richard Lee supports the idea of redundancy in talking about a general subsistence strategy:

> Wherever two or more kinds of natural foods are available, one would predict that the population exploiting them would emphasize the more reliable source. We would also expect, however, that the people would not neglect the alternative means of subsistence (Lee and DeVore, 1968:41).

Lee's comment will be returned to in the final evaluation of the options. For now, however, the implication of redundancy for the human population is that it would be impossible to rely completely on one resource. The unpredictability of animal resources in the Keewatin that was described previously should make the application of Alland's concept clear.

A more extended comment in regard to fish and why they may be eliminated as a feasible single option might be appropriate here. Fish seem to be a special case in that they are a relatively stable, plentiful, and easily caught resource:* a human population might have focused on this predictable, widely distributed resource. Rostlund suggests that per unit area, the water "undoubtedly produced more food than did the land" (1952:6).

Notwithstanding this abundance, fish are not a reliable resource. In the first place, northern lakes are not rich in fish food, so the fish have to be on the move looking for it. Fish are likely to be unpredictable in their movements and distribution, at least in summer (Clarke, 1940:120) and probably in winter. Rarely is there such a concentrated and locally dependable fish population that permanent year-round settlements might be feasible (Rostlund, 1952:30). "There are . . . times when the lakes and rivers are well supplied with fish . . ." but "they are not capable of supporting a substantial intensive fishing effort" (Clarke, 1940:120). Although Clarke was talking in terms of commercial fishing, his comments can be applied to people who might rely on fishing for subsistence using a relatively primitive fishing technology. Furthermore, there can be very

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*Winter ice-fishing requires a higher expenditure of energy than does fishing in open water, since one must chisel and keep open holes in great thicknesses of ice.

poor years for fish in even good spots (Harper, 1948:154). The sparse fish resources make possible "fishing out" a lake, taking so many fish that the population takes several years to recover, although this possibility is especially related to commercial operations. Samuel Hearne summarized the problem when he described the reliance he felt could be put on this option:

> It is true, that few rivers or lakes in those parts are entirely destitute of fish; but the uncertainty of meeting with a sufficient supply for any considerable time altogether, makes the natives very cautious how they put their whole dependence on that article, as it has too frequently been the means of many hundreds being starved to death ([orig. 1795], 1958:47).

"Small game" might also seem to be an exception, since as a category it can include several different animal species. Like fish, they are all too unpredictable and variable in availability to make reliance on them alone a feasible strategy. Further, too many animals would be required for communal feeding.

The single resource options can therefore be eliminated: for the tundra, the summer options of musk-ox only, fish, small game, and caribou (#1,2,3,4) and the winter options of musk-ox, fish, and small game (#1,2,3). In the forest the summer options of moose, fish, and small game (#1,2,3) and the winter options of moose, fish, small game, and caribou (#1,2,3,4) are eliminated.

The number of remaining options is quite small, with eleven summer options for the tundra and only one winter

option, while there are four summer options for the forest and eleven winter options (see Table 6). The number of species involved is listed in Table 6 in parentheses (ducks, geese, and swans count as one for this purpose).

Finally, as combinations of resources are considered desirable, it might help to consider those options that are compatible, that is, those that could be exploited simultaneously by people living in one habitat. Because of the nature of the vegetation and animal distribution, all the tundra options, summer and winter, are compatible. The summer options in the forest are compatible since the small game is mostly that found in moose habitat. For the forest in winter there are three sets of compatible resources, with the first and second being subsets of the third. The first includes those animals oriented to successional vegetation, comprising combinations of moose, fish, and small game (options #5,6,7,15). The second includes animals oriented to climax conditions, comprising combinations of caribou, fish, and small game (options #9,10,11,15). The former involves fifteen species; the latter, nine, with the difference deriving from the small game category (see Table 7). Finally, the third set includes both successional and climax options (options #8,12,13,14 in addition to the preceding ones). Moose and caribou live in mutually exclusive habitats, as does the small game associated with each. However, their respective habitats are interdigitated, an effect caused by

Table 6

REVISION #2: NUMBERS OF ANIMAL OPTIONS

Season	Summer	Winter
Zone		
Tundra	11 (12)	1 (7)
Forest	4 (15)	11 (18)

The number of species involved is listed in parentheses.

Table 7

REVISION #3: NUMBERS OF ANIMAL OPTIONS

Season	Summer	Winter	
Zone			
Tundra	11 (12)	1 (7)	
Forest	4 (15)	Successional habitats 4 (15)	Climax habitats 4 (9)
		Total: 11 (18)	

Number of species involved is listed in parentheses.

the small, local nature of fires. Both moose and caribou could therefore be hunted from one base, increasing the "redundancy" of the system. The edge effect resulting from the mosaic pattern of vegetation would almost certainly be especially important for a human population since it doubles the potential options.

Adaptive Strategies

It is from these remaining sets of options that a probable adaptive strategy or strategies must be hypothesized. An adaptive strategy involves essentially the yearly round of subsistence activities, the exploitative pattern. There are three questions that must be answered to complete this part of the analysis:

1. In which zone would people live?
2. What options would they exercise there?
3. How would they use these options?

Because an adaptive strategy may involve different options at different times of the year and because of the strong seasonal differences in the Keewatin, each question actually becomes two, one for summer and one for winter. The answer to the question of where people would be located is of course determined by the options available to them in each zone.

Winter Adaptive Strategies

The choice of winter location is easily deduced from the choice of winter options and species in the two subzones

In terms of both options and species, the Lichen-Woodland Subzone is far richer than the Shrubby Tundra. To try to live on the tundra in winter would be reducing the number of available alternatives to an impossibly narrow margin for survival. Also, there are fewer sources of fuel for warmth and cooking. Hanbury said that "to penetrate this country [tundra] in the dead of winter would be simply to court starvation" (1904:13), a not unreasonable appraisal. Therefore on can assume that the aboriginal human population must have lived in the Lichen-Woodland during the winter.* One must assume also that in an area as impoverished not only in number of species but also in the actual number of animals as the Keewatin, all mutually compatible options would have been exercised simultaneously when possible. Further, one would assume, following Lee (above), that the population would emphasize or orient itself to the most reliable of food

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*Historically there existed a counter to the argument presented here: the Caribou Eskimos lived year-round in the interior tundra with little dependence on coastal resources. They had an extremely marginal subsistence base and were often in danger of starvation. I would suggest that such an adaptation developed either in response to a temporary period of animal abundance inland or as the result of the elimination of coastal possibilities, for whatever reason. Either possibility would have led to a dependence on the caribou and fish aspect of a previous adaptive strategy. Further, by relying on a single zone strategy in an area characterized by such fragile ecosystems, the Caribou Eskimos would probably have died out eventually or would have reintegrated coastal resources into their adaptive strategy. Archeologically it does not appear that Caribou Eskimo culture had any great antiquity.

resources. In the forest the most reliable are caribou and fish, not moose or small game (see below). Fish are probably the most reliable complementary resource, but because they cannot be relied upon as a primary resource, and because animals are needed for their hides and bones as well as for their flesh, caribou are the key winter game resource.

Moose are less reliable in the Lichen-Woodland winter and consequently a less feasible resource because they are so few in number compared to caribou. Large moose populations exist only where a region has a steady supply of vegetation in early successional stages. It is quite conceivable that at some point in the past repeated burning created enough successional vegetation with good quality browse for a long enough time to allow a successful moose invasion of the Lichen-Woodland Subzone. The evidence now available indicates, however, that post-fire browse is not usually that most suitable for moose (Rowe and Scotter, 1973:458), and that most fires are small and localized. Further, whatever suitable pasture is created by fires disappears quickly by growing out of reach if there are no "nucleus herds" of moose in the area to exploit it (Spencer & Chatelain, 1953: 541). Therefore, moose were likely uncommon in this subzone until some time within the last century. This conclusion is supported by observations (Peterson, 1955:36-43; Mercer and Kitchen, 1968; Preble, 1908:132; Harper, 1956:75; Soper, n.d.: 45; Banfield, 1951a:119; Harper, 1932:30; Clarke, 1940:28;

Hornby, 1934:108). The small game associated with moose would have been less reliable also in that not only do they depend on cycles of successional vegetation, but they themselves are cyclic as well.

The carrying capacity of the land seems to be less for moose than for caribou, in addition. The size of moose populations could never equal that of caribou even if the proportion of climax vegetation to successional vegetation were markedly different from that necessary to support the good-sized caribou wintering herds of the historic past. However, there is not information available on differences in pounds of meat per acre that could be supported, so this apparent difference in numbers of animals may be misleading in terms of carrying capacity.

The advantages of moose are that they may be more evenly distributed than caribou, and in the winter especially they can be easily tracked or run down. Moreover, each moose is the equivalent of many caribou in terms of weight. Their overall small population size acts against choosing moose as a key resource, however, unless one assumes that the human groups are themselves scattered and small in size. Since this assumption cannot be made, it is simpler to deal with moose as an alternate option in terms of a caribou oriented strategy, to be discussed later.

An Emphasis on Caribou

The evidence that moose were uncommon in the Lichen-

Woodland means that caribou are therefore the more plausible resource. In the winter it would thus be the climax set of options (#9,10,11,15) that would be preferentially exercised, leaving the successional set (#5,6,7,15) as an alternative.

If the most feasible winter adaptive strategy would have been one based on the barren-ground caribou, how would this and the other compatible options have been exercised? Also, at what points would the alternative set of options, also compatible, be put into use?

The first factor to be considered is that caribou travel hundreds of miles during their yearly wanderings between forest and tundra and within each zone. They also change their routes and pastures. "The vagility of tarandus individuals and herd ensures that without highly modernized means of conveyance, such as aircraft, snowmobiles, or 'weasles,' humans cannot 'move with the caribou' in any literal sense" (Burch, 1972:345), on a year-round basis.

It is nearly impossible to dog their paths at all seasons. By what other strategy could this resource best be exploited? A canny hunter would try to be wherever he most expected the caribou to appear, which is what Burch calls the "head-'em-off-at-the-pass" strategy (1972:346). Caribou movement is especially predictable during the fall migration when they have to cross major obstacles by fording lakes and rivers at locations such as narrows. Another strategy would be Burch's "search and destroy" technique, which involves

actively seeking out the animals in areas or at times of the year when they are apt to be relatively sedentary or when they prefer a very specific set of environmental conditions, such as at the height of the fly season and during the coldest parts of winter (Burch, 1972:347). Each strategy is reasonable at certain times of the caribou annual cycle.

Considerations other than strategy are changes in the physical condition of the caribou as they move trough their annual cycle which are important to people wishing to use them for food and clothing. In late spring and summer their meat is lean and stringy, with little fat except in the tongue and marrow. Insect harassment keeps them from eating properly, and they are at their lowest physiological point during the August dispersal. Hanbury remarked that caribou meat in early August "was wretchedly poor" (1904:39). As fall nears, insects disappear, and the caribou are able to relax ans start feeding in earnest. This period allows them to form fat deposits. By the time they reach treeline in their fall migration (end of August through September), they are in fine physical shape (Kelsall, 1968:131,211). The bulls are especially prime then because they have developed a saddle, or <u>depouille</u>, of backfat. By the end of the rutting season (end of October) they are again in poor condition. At this time, the females are considered the better game, but the cows start showing the <u>depouille</u> only towards the end of the year, and never as much as the males (Pike, 1892:50).

The condition of the hide also varies. Pike suggested that the best skins for "hair-coats" should be taken from the young caribou in July or August (1892:50), while Hearne thought that late August or early September was the best season ([orig. 1795], 1958:32,127). Banfield explains that the warble fly scars would have healed by early autumn (1951b:32). Also, by autumn the caribou would be acquiring their thick, warm, winter coats. However, if hides are taken too late--Hearne said that mid-October was the last acceptable date--the hair would be too long and loose and would drop off the skin easily (Hearne[orig. 1795], 1958:127). The prime season for hides thus corresponds roughly with the prime season for meat, the fall when the caribou are moving near the treeline or actually migrating into the forest.

Fall sees the convergence of many different elements relevant to subsistence options: it is the best season for caribou meat and hides as well as the easiest time to intercept caribou, using Burch's first strategy. Ducks, geese, and swans are migrating south in large flocks, and berries are in season. Moreover, it is the season when whitefish and lake trout spawn, though they are at their nutritional low when spawning. Nevertheless, great numbers of fish in good condition could be taken during the early part of their runs (McPhail and Lindsey, 1970:84,113,140; Wynne-Edwards, 1952:13,16; Clarke, 1940:120; Harper, 1948:167). The cooling weather might enable easier preservation of meat

through freezing, though rainy weather would make drying fish and meat difficult.

What are the implications of these considerations for a winter adaptive strategy? The first is that the human predators would try to make a large kill in the fall (late August through September) when the meat and hides are prime and easily preserved. The hunters would station themselves at river or lake narrows which the caribou cross during their migration. These crossings and kill sites would necessarily be located near the treeline, or perhaps in the Forest-Tundra Subzone. Caribou are especially easy to kill when they are swimming, and they can be snared along the shore. A hunter who had correctly predicted their crossing point would be able to slaughter as many as desired in this ideal situation.

While they were waiting for the caribou to migrate, these groups would have had to rely on other resource options for food. They include small game, especially migratory birds, and most importantly, fish, the most dependable secondary resource. It would be reasonable to expect hunters to wait at narrows that would also supply fish, at one part of a large lake. There they could also dry and freeze fish, lending survival if the caribou chose a different migratory route that year.

If the people had some means of transporting the meat and hides they had accumulated, they could follow the caribou into the forest, adding more to their supply as they

went. There would have been technological limits on travel, however. Canoes in summer and sleighs in winter would have been the only forms of transportation before the advent of planes and trucks. Canoes are impractical because of the drainage system which makes rivers virtually unnavigable without numerous portages. When they can be used, canoes can carry only a limited amount of cargo beyond the human occupants. Moreover, at this time of year caribou are crossing waterways, not following them. Sleighs likewise are of limited use. They are restricted to periods when there is adequate snow cover, and they have to be pulled by either humans or dogs, assuming that the caribou were not domesticated.

While dogs might be useful for pulling sleighs or carrying packs and for hunting, they could also be a considerable burden in times of food scarcity unless they were killed for food. Dogs can be turned loose to forage on small game up to a point, but this solution of abandoning them for a season would be impractical unless the human group travelled the same route each year. For the most part, more than a few dogs would probably be an extra burden in terms of the technoenvironmental advantage of the total system.

For those who had had successful hunts, dogs would not be necessary because their best course of action in terms of energy output would be to stay at the narrows as long as their supply of meat lasted. If the "harvest" had been

especially good, and if the weather allowed preservation, a group of people could conceivably stay in that vicinity for much of the winter, although they could also cache meat and continue moving after the caribou. In any event, at some time they would have to camp long enough to prepare some of the hides, not something easily done on the move.

The people who moved most in the winter would probably be those who had not been successful in the fall hunt, either because a few caribou had passed their way or because they had missed the migration completely. These individuals would be forced to move deeper into the forest, scattering out in small groups to optimize their chances of finding the caribou that were also scattering at this time. They would almost certainly exercise the alternative set of options, hunting moose, small game, and fish as well as caribou, thus increasing their resource possibilities and increasing the redundancy of their adaptive strategy. Their camps would consequently need to be located in ecotonal areas, especially those near lake shores, which would give them potential access to fish and aquatic rodents. Camps might also be located with an eye to good sources of wood for fires. Caribou can often be found resting on lakes as well. Dogs would only be a liability for people who were short of food, and the people would likely have to pull their sleighs themselves, limiting the amount they could haul.

Late winter would be a period of scarcity and even starvation. January through March are the worst months for

fishing because of the thick ice. Caribou may be scattered across a wide territory, or they may be massed in a few good feeding areas, not necessarily easy to locate. Further, they are much harder to hunt when they are in small groups or when it is very cold (Burch, 1972:361). Even people who did well in the fall hunt and throughout the early winter might be running short of food by this time. In February and especially towards April the female and young caribou begin to form large herds again near the edge of the forest, preparatory to spring migration. This time their movements are far less predictable because they will leave the forest from wherever their winter movements have taken them. Even if the land is in thaw, the lakes and rivers are still frozen, imposing no water barriers to funnel their migration. The caribou walk along the lakes when they are oriented in the direction of the calving grounds.

During late winter the human population would probably move toward the treeline also, if they had not wintered there, while searching for caribou and other game. Although caribou would again be in large herds, one would anticipate finding the people spread out along the edge of the woods, hoping to intercept some animals. With fish in short supply, there would be no abundance of food to allow large numbers of people to congregate in one place until after a large kill had been made. There would be an especially heavy reliance on the small game option, and this

time would be when people would certainly be exercising the successional set of options if they had not already been doing so before.

As long as the land remained frozen, people would be able to move about fairly freely. During spring thaw, they would be restricted to high ground while the caribou continued to move out of the woodlands ahead of them. During this period one of the most important sources of food would probably be the returning migratory birds, fat from wintering in more southerly regions. The end of the thaw and break-up would find the female caribou and young caribou far out on the tundra, nearing their calving grounds, and the males would remain behind them closer to the forest. By the end of migration, if not before, caribou have lost their fat deposits (Kelsall, 1968:41). Both meat and hides are in poor condition for consumption until the following autumn.

Summer Adaptive Strategies

The winter adaptive strategy has covered fall and spring strategies too, with the fall strategy the key to the winter activities which follow it. The spring strategy may be one key to the more complex problem of summer strategies. Analytically, summer is a complex season in that both zones appear to offer about the same number of species and resources. The tundra offers the greater number of options, but the forest can be expected to be richer in numbers of animals. Therefore both tundra and forest should be

considered as possible locales for human occupation. The alternatives are (1) that the human population could continue following the caribou and move out onto the tundra for the summer, or (2) that they could stay within the forest.

A human population that chose to stay within the Lichen-Woodland Subzone would be faced with many of the same problems as a group who chose to exercise the winter successional set of options only, the most important of which is that the number of herbivorous animals available would depend on the amount and type of successional vegetation. However, fish would be plentiful and readily available, which could offset animal shortages. Therefore fish would be the most reliable resource, and human movement in the woodland would tend to be oriented toward fishing lakes.

Large and/or very good fishing lakes could conceivably support large concentrations of people, but not permanently. One would expect that small, impermanent groups would be a more usual pattern, with people staying at a lake for as long as the fishing remained good. This pattern would change in the fall, with people moving toward the tundra or perhaps into the tundra fringe to intercept the caribou migration at various points.

A population that followed the caribou onto the tundra after the end of spring thaw would have access to small game, especially birds and their eggs, and to fish, as in the forest. Furthermore, they would have access to not

one but two large herbivores, caribou and musk-ox. Caribou meat is very poor food during the summer, and the people would probably resort to fish, small game, and musk-ox for an important part of their diet. By following the caribou during this season they would have a fairly good idea about the migration route they might expect them to take in the fall. As the caribou began to form their fall migration herds, they would be better able to anticipate their movements so as to station themselves at a good fish lake with a caribou crossing where they could take large numbers of both. This latter summer strategy could support large groups of people on the move most of the time, or small, stationary groups.

Both strategies seem feasible. The differences between the tundra and forest are probably not significant in that summer is generally a season of relative plenty (compared to winter) in both regions. Spending the summer on the tundra seems to be desirable for three reasons: first, if a population had hunted the caribou throughout the winter, when spring came they would be in location and be able to follow behind them.

Secondly, there is the emphasis placed on the essential fall caribou hunt. It would be adaptive to follow the caribou throughout the summer so as to know about where they would be in the fall. The caribou are not travelling especially rapidly in the summer, and a group of people should be able to keep up with them.

Finally, larger numbers of people could be supported more successfully if they used the resources of each zone for only half the year rather than depending upon them for the whole year. In other words, the "carrying capacity" of the land for human predators would be greater if they were migratory. Even if they were relying on different resources during the different seasons, there would still be some resource overlap, especially of fish.

On the other hand, there are two good reasons for spending the summer in the forest. The first is that the number of animals is geater, and the second is that it would be less costly in energy expenditure to stay put in one or a few camps than to be continually on the move following the caribou. The main problem with this strategy would be that it would make the fall carbou hunt more risky.

Because of this problem, I would guess that the preferred summer adaptive strategy would be to follow the caribou on to the tundra, returning to the forest in the fall, a pattern of parallel annual migrations. Nevertheless, remaining in the forest would be a feasible strategy. Therefore the question of which strategy would be adopted can be at best only partially resolved.

Summary: Two Adaptive Strategies

To summarize, there are two feasible adaptive strategies that could have been adopted by the aboriginal human population. Both share the same winter pattern,

relying on caribou for the duration of the winter, when possible. Relying on caribou implies that at the same time there were alternative food sources, especially fish in the fall and small game in the spring, as well as moose throughout the winter. Fall could be an especially productive period in that it was the peak period for both hunting and fishing. These alternative resources could be considered support strategies.

The two strategies differ in their summer patterns: one is that of moving onto the tundra following the migrating caribou. Caribou may not have been the most desired prey at that time, but they would have oriented a group's movement while they sought other game, especially fish, small game, and musk-ox. A group moving with the caribou would be in the best position to intercept a herd in its fall migration.

The alternative to summer on the tundra would be to spend it around a fish lake or a series of fish lakes in the forest, hunting small game and moose. The group would then have to move in the fall to where they anticipated finding the migrating caribou. This summer strategy would have been far more sedentary than the former. Such a sedentary pattern foreshadows later fur trade adaptations that involved summer concentrations of people in the vicinity of a trading post in the forest.

Looked at more broadly, these two adaptive strategies are themselves variations on a more inclusive single strategy

that encompasses all possibilities to provide greater flexibility and maximum redundancy in an area characterized by an impoverishment of resources. It would be maladaptive for a human population to restrict itself to only one of these possibilities. Instead, one might expect to find both strategies followed at different times.

Demographic Implications

These two subsistence strategies suggest parallel demographic distributions. Fall would be characterized by large aggregates of people waiting for the caribou. If the hunt were good, the group might be lone lasting; if hunting and fishing were poor, it would break up into smaller units to cover more territory and maximize chances of finding game throughout the winter. Spring was again probably a time of dispersal and of slim resources, corresponding to small social units.

The tundra would provide a number of alternatives for exploitation in the summer: people could live together in small or large groups as they pleased, though large groups could probably not have been sedentary. The local food supply did not impose a group size, in other words.

Spending the summer in the forest, on the other hand, would possibly force people to live in reasonably small groups since their main resource would be fish lakes and whatever hunters could find in the vicinity. A large fish lake could support a large number of people, and large groups

could collect for fish runs, but the usual pattern would likely be one of small units of people unless there were enough moose in the area to support large gatherings.

One further demographic implication pertains to general groupings of people within the entire region. If the aboriginal inhabitants were oriented toward the caribou on a year-round basis, they would have been oriented toward one of three separate caribou populations: Kaminuriak, Beverly, or Bathurst. The effect of this orientation would have been to divide people into three corresponding regional populations. The same situation would have been the case for people who stayed in the forest during the summer, since they would have to be in striking distance of one or the other populations during fall migration.

CHAPTER 4

CONCLUSION

A major problem in Northern Athapaskan studies has been that the aboriginal lifestyle may have changed rapidly in response to contact with Europeans and the fur trade. Because of the lack of early, intensive historical documentation, it has been virtually impossible to distinguish pre-contact cultural traits from those of the post-contact period. Athapaskanists have either ignored this problem or, worse, have confounded it by regarding the aboriginal culture as simply an earlier manifestation of that of the ethnographic present. The purpose of this paper has been to show that at least some bases of aboriginal Dene lifestyle could be hypothesized by examining man-environment relations, developing "a model of probable pattern of resource use based on the possible adaptations to the various ecosystems . . ." (Intro. p. 5). Such a model would represent something similar to Steward's "local potentialities" resulting from "'the interaction of environment, exploitative devices, and socioeconomic habits'" (Steward in Harris, 1968:659); in other words, the adaptive strategy. The pattern of resource use or "'the exigencies of making a living'" (Steward in Harris, 1968:659) determine to a certain degree or at least set limits on demographic groupings and the yearly round of

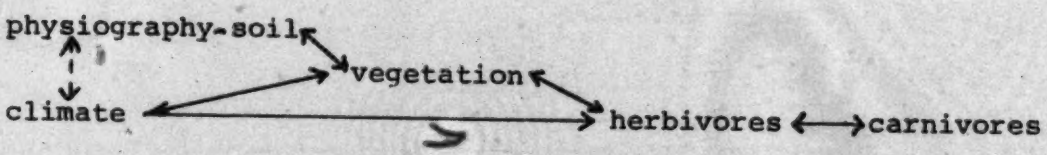
movement.

The first step in deducing the local potentialities involved an examination of the vegetation, fauna, and the factors affecting their distribution. People living off the land must have had a commonsense understanding of significant environmental features. Therefore to ignore this part of such a group's culture would be to make an economic analysis or an analysis of adaptive strategy abstract to the exclusion of local and regional variability (scientifically this variability is constantly demonstrated by this study).

The relationship among physiography, climate, vegetation, and fauna can be depicted graphically, as in Chart 5.

CHART 5

Interrelationships: Ecosystem Components



A poor substrate for plant growth and the extreme temperature seasonality of the region determine the Keewatin's three vegetation subzones, the Tundra, the Forest-Tundra, and the Lichen-Woodland. Each is composed of a number of plant communities characterized by distinctive fauna. In other words, each is a biotic community or biome.

Even in this relatively uncomplicated area, the

patterning of vegetation and fauna is quite intricate. On the tundra, the various plant communities are distributed in mosaic fashion. Consequently, they and the animals depending on them are characterized by this interdigitation, and there are no regions or zones restricting animal location. The important resource animals of the tundra include the musk-ox, the barren-ground caribou (summer only), small game, especially birds (mainly summer), and several species of fish.

In the forest the vegetation is divided into two discrete, interdigitated categories, one containing climax plants and the other, successional plants. Climax vegetation is typically spruce-lichen or pine-lichen forest, which barren-ground caribou inhabit in the winter. Fish and some small game can also be found in climax regions. Successional vegetation is characterized by plants such as grass, herbs, shrubs, and young trees, especially the deciduous birch, aspen poplar, and balsam poplar. It supports a spatially distinct configuration of animals: moose, much small game, and fish. Although moose is a species typically associated with the successional vegetation, especially willows, these are not necessarily related to post-fire succession. Moose seem to have been uncommon in the Lichen-Woodland Subzone until the last century for reasons that can only be hypothesized, not clearly determined.

The second step in the analysis involved deducing the possible ways a human population could use the resources

found within the habitats. In the Introduction some general parameters for the human population were established, namely, that they were primarily hunters and fishers operating at a lithic-bone level of technology. For these people, there are two adaptive strategies that seem most feasible.

The winter strategy is based on the premise that at that season people must live in the forest since the tundra with its harsh climate presents too few resource options for survival. The fall adaptive strategy is the key to the winter pattern, since during fall the most logical resource to exploit is the massive caribou migration into the forest as they cross lakes at narrow places. At this time the caribout meat and hides are prime, and the animals are both numerous and easy to hunt. Fish would be a necessary complementary resource, ensuring survival if the caribou hunt were poor. This strategy would allow and encourage the congregation of large numbers of people.

There are two possibilities for winter, each variants of a basic strategy based on an orientation to the barren-ground caribou. Those people who had had a good fall hunt might remain at or near the kill site, since they lacked the capacity to transport the wealth of meat and hides they could accumulate. Conversely, people who had had a poor fall hunt would have moved farther into the forest, looking for the caribou. This latter group would exercise additional options, hunting small game, moose, and fish as well as

caribou. People practicing both variants would probably be hunting small game heavily in late winter and spring, times of resource scarcity. Though people might still be following the caribou, there would be less certainty of finding them. Therefore, in winter and spring smaller social units would be adaptive.

The winter season offers little choice to hunters in terms of adaptive strategy. In summer, on the other hand, there are two distinct choices, both feasible. The first involves a group's continued orientation toward the caribou, following the caribou onto the tundra and trailing after them throughout the summer so as to be able to improve their chances of intercepting them for the crucial fall hunt. Since caribou are poor game during summer, however, other prey such as fish, small game, and musk-ox might have been more desirable. Social units could be either large or small; the resource base would not determine one or the other.

Should a group choose to stay in the forest for the summer, they would be able to fish and to hunt small game (including game birds) and moose. They would be oriented toward fish primarily as their most reliable resource. They would also be much more sedentary than people using the other summer strategy, and their social units would likely be small.

The emphasis in this paper has been on the economic "habits" that might have been necessitated or limited by the resources of the area. The social "habits," the other part of Steward's "socioeconomic habits," have remained unknown

although they were certainly most important in mediating between the alternatives. Samuel Hearne's Chipewyans were following caribou on a year-round basis, yet they could have stayed in the forest in the summer just as easily. This pattern did in fact occur with involvement in the fur trade.

Besides its more obvious function of predicting habitation or kill sites, this paper should show that one cannot simply extrapolate from natural history data or from the historic period backwards in time. Because a degree of choice was present, the aboriginal situation cannot be simply interpreted from ethnohistorical data. Even if it could be assumed that the immediate ancestors of the contact population had the same values as post-contact Chipewyans and Yellowknives, it cannot be assumed for much older populations, who lived with the same possibilities.

In conclusion, then, it is possible to demonstrate possible adaptive strategies and some of their demographic consequences within a certain degree of probability. In other words, a range of possibilities for a human population can be established given the nature of the environment. These possibilities should encompass most actualities. The actual strategy used by a particular group of people, the result of cultural mediation, must be determined by other means, however, using archeological and ethnohistorical data to resolve the problem once the underlying possibilities are known.

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APPENDIX A

KEEWATIN ANIMALS: BIBLIOGRAPHIC REFERENCES

I. MAMMALIA

Insectivora

Family Soricidae

1. Common masked shrew (Sorex cinereus): Harper, 1956: 11-12; Soper, n.d.:11.

2. Arctic shrew (Sorex arcticus): Soper, n.d.:11.

3. Tundra shrew (Sorex tundrensis): Preble, 1908:246.

4. Pygmy shrew (Microsorex hoyi): Preble, 1908:247.

Lagomorpha

Family Leporidae

1. Snowshoe hare (Lepus americanus): Harper, 1956:16; Harper, 1932:29; Soper, n.d.:15; Kiris, 1959:47; Hornby, 1934:109; Shelford and Olson, 1935:39.

2. Arctic hare (Lepus arcticus): Harper, 1956:13-14; Harper, 1932:29; Soper, n.d.:15; Preble, 1908:207.

Rodentia

Family Sciuridae

1. Hudson Bay chipmunk (Eutamias minimus hudsonius): Banfield, 1951a:117; Soper, n.d.:19; Preble, 1908: 16.

2. Parry's ground squirrel (Spermophilus undulatus parryii): Harper, 1956:17; Banfield, 1951a:116.

3. Red squirrel (Tamiasciurus hudsonicus): Harper, 1956: 18-24; Harper, 1932:27; Banfield, 1951a:24,117; Soper, n.d.:20; Shelford and Olson, 1935:393; Fairbairn, 1931:159; Kiris, 1959:47.

Family Castoridae

4. Beaver (Castor canadensis canadensis): Harper, 1956:24; Harper, 1932:28; Banfield, 1951a:117; Soper, n.d.: 20-22; Preble, 1908:194-195; Pennant, 1784:103; Larin, 1959:156; Hewitt, 1921:232.

Family Cricetidae

5. Arctic white footed mouse (Peromyscus maniculatus borealis): Harper, 1932:28; Fairbairn, 1931:159; Preble, 1908:175.

6. Boreal red-backed vole (Clethrionomys gapperi): Harper, 1956:29-35; Harper, 1932:28; Soper, n.d.:26-27; Preble, 1908:178-179; Elton, 1942:448.

7. Tundra red-backed vole (Clethrionomys dawsoni): Soper, n.d.:26; Banfield, 1951a:118; Preble, 1908:180-181; Pitelka, 1967:162.

8. Mackenzie spruce mouse (Phenacomys ungava mackenzii): Harper, 1956:35-40; Soper, n.d.:28; Preble, 1908:177.

9. Meadow vole (Microtus pennsylvanicus): Harper, 1956:40-43; Banfield, 1951a:118; Soper, n.d.:28; Preble, 1908:186.

10. Chestnut-cheeked vole (Microtus xanthognathus): Soper, n.d.:29; Preble, 1908:188.

11. Muskrat (Ondatra zibethicus albus): Harper, 1956:43-45; Harper, 1932:28; Banfield, 1951a:119; Soper, n.d.: 29-30; Preble, 1908:191-193; Fairbairn, 1931:160; Shelford and Olson, 1935:391; Hewitt, 1921:232; Keith, 1963:43.

12. Brown lemming (Lemmus trimucronatus trimucronatus): Harper, 1956:29; Soper, n.d.:26; Preble, 1908:181; Pitelka, 1967:153,160.

13. Northern bog lemming (Synaptomys borealis): Preble, 1908: 183.

14. Varying lemming (Dicrostonyx groenlandicus): Harper, 1956:25-29; Banfield, 1951a:117; Soper, n.d.:24-25; Elton [orig. 1942], 1965:440; Pitelka, 1967:153,160.

Family Zapodidae

15. Hudson Bay-jumping mouse (Zapus hudsonius hudsonius): Soper, n.d.:31-32.

Family Erethizontidae

16. Porcupine (Erethizon dorsatum dorsatum): Soper, n.d.:32; Preble, 1908:197; Shelford and Olson, 1935:390.

Artiodactyla

Family Cervidae

1. Moose (Alces alces andersoni): Harper, 1956:75; Harper, 1932:29-30; Banfield, 1951a:119; Soper, n.d.:45; Peterson, 1955; Preble, 1908:130-134; Hornby, 1934: 108; Shelford and Olson, 1935:384; Clarke, 1940:28; Hewitt, 1921:53; Fairbairn, 1931:159; Spencer and Chatelain, 1953.

2. Eastern woodland caribou (Rangifer caribou): Harper, 1932:31; Preble, 1908:135; Clarke, 1940:30.

3. Barren-ground caribou (Rangifer tarandus): Banfield, 1951b; Harper, 1955; Kelsall, 1968; Parker, 1971, 1972a, 1972b; Burch, 1972; Thomas, 1969; Preble, 1908; Formozov, 1946:131; Pruitt, 1959.

4. Wood bison (Bison bison athabascae): Preble, 1908:143; Hewitt, 1921:114-131.

5. Barren-ground musk-ox (Ovibos moschatus moschatus): Harper, 1956:78; Harper, 1932:35; Soper, n.d.:47; Hewitt, 1921:90-99; Preble, 1908:150; Hornby, 1934: 107; Pennant, 1784:10.

Carnivora

Family Canidae

1. Tundra wolf (Canis lupus hudsonicus): Harper, 1956:47-51; Banfield, 1951a:116; Soper, n.d.:34; Clarke, 1940:36; Hornby, 1934:108; Preble, 1908:213; Hewitt, 1921:225.

2. Timber wolf (Canis lupus griseoalbus): Harper, 1932:26; Soper, n.d.:34; Preble, 1908:211; Shelford and Olson, 1935:387; Hewitt, 1921:225.

3. Arctic fox (Alopex lagopus innuitus): Harper, 1956:57-59; Harper, 1932:25; Banfield, 1951a:114; Soper, n.d.:35; Clarke, 1940:35; Preble, 1908:217; Hornby, 1934:108; Hewitt, 1921:228; Keith, 1963:47; Elton, 1965:272.

4. Red fox (Vulpes fulva regalis): Harper, 1956:59-60; Harper, 1932:25; Banfield, 1951a:114; Soper, n.d.: 35; Clarke, 1940:35; Hornby, 1934:108; Preble, 1908: 215-216; Hewitt, 1921: 222-223; Keith, 1963:47.

Family Ursidae

5. Black bear (Euarctos americanus americanus): Harper, 1956:61-63; Harper, 1932:22; Banfield, 1951a:114; Soper, n.d.:35; Preble, 1908:220; Shelford and Olson, 1935:387; Fairbairn, 1931:160; Hewitt, 1921: 232.

6. Anderson's grizzly (Ursus andersoni): Harper, 1956:64; Harper, 1932:23; Banfield, 1951a:114; Hewitt, 1921: 107-108; Preble, 1908:224; Hornby, 1934:109.

Family Mustelidae

7. Pine Marten (Martes americana abieticola): Harper, 1956: 64-65; Banfield, 1951a:116; Soper, n.d.:36; Preble, 1908:234; Clarke, 1940:33; Shelford and Olson, 1935: 393; Fairbairn, 1931:160; Pennant, 1784:77; Larin, 1959:154-155; Elton [orig. 1942], 1965:273; Hewitt, 1921:228; Keith, 1963:50; Hawley and Newby, 1951:182.

8. Fisher (Mates pennanti pennanti): Soper, n.d.:36; Shelford and Olson, 1935:391; Preble, 1908:238; Hewitt, 1921:229.

9. Richardson's weasel (Mustela erminea richardsonii): Harper, 1956:65-68; Harper, 1932:23; Banfield, 1951a: 116; Soper, n.d.:36; Shelford and Olson, 1935:391; Preble, 1908:231-232; Clarke, 1940:34; Fairbairn, 1931:160; Elton [orig. 1942], 1965:448.

10. Least weasel (Mustela rixosa rixosa): Soper, n.d.:37; Preble, 1908:234.

11. Mink (Mustela vison lacustris): Harper, 1956:68-70; Harper, 1932:23; Soper, n.d.:37; Shelford and Olson, 1935:391; Preble, 1908:229; Hewitt, 1921:230; Keith, 1963:50,67.

12. Wolverine (Gulo gulo luscus): Harper, 1956:70-71; Harper, 1932:23-24; Banfield, 1951a:116; Soper, n.d.:37; Preble, 1908:239; Shelford and Olson, 1935:387; Hewitt, 1921:232; Hornby, 1934:108.

13. Skunk (Mephitis hudsonica): Harper, 1932:24; Preble, 1908:227.

14. Otter (Lutra canadensis preblei): Harper, 1956:71-73; Harper, 1932:24; Preble, 1908:228; Pennant, 1784: 87; Clarke, 1940:35; Harris, 1968:50,53,60-61,204-206; Hewitt, 1921:232.

Family Felidae

15. Lynx (Lynx canadensis canadensis): Harper, 1956:73-74; Harper, 1932:26; Soper, n.d.:40; Preble, 1908:209-210; Clarke, 1940:36; Shelford and Olson, 1935:387-390; Hewitt, 1921:219-220; Keith, 1963:44-46; Heinselman, 1971:65.

II. AVES

Galliformes

Family Tetraonidae

1. Spruce grouse (Canachites canadensis): Shelford and Olson, 1935:393; Preble, 1908:37-39; Fairbairn, 1931:161; Scotter, 1964:78.

2. Ruffed grouse (Bonasa umbellus): Preble, 1908:340; Fairbairn, 1931:161; Keith, 1963:23-24.

3. Sharp-tailed grouse (Pedioecetes phasianellus): Prebles, 1908:348; Scotter, 1964:78.

4. Willow ptarmigan (Lagopus lagopus): Preble, 1908:342; Hornby, 1934:110; Clarke, 1940:48.

5. Rock ptarmigam (Lagopus mutus rupestris): Preble, 1908: 347; Hornby, 1934:110; Clarke, 1940:48; Keith, 1963:68.